Notes on Atlantic and other Asteroidea. 1. Family Benthopectinidae

GENERAL
5 NOV 19
LIBRARY
RAL HISTO

Ailsa M. Clark

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Contents

Synopsis 91
Introduction 91
Systematic discussion 91
Family Benthopectinidae 91
Genus *Cheiraster* 107
Genus *Pectinaster* 118
Genus *Benthopecten* 122
Acknowledgements 134
References 134

Synopsis

Various taxa of the family Benthopectinidae, mainly from the Atlantic, are reviewed. The genera *Pectinaster* and *Cheiraster* are redefined, *Pectinaster* being restored to Perrier's concept of 1894 by transfer of several nominal species without specialized papularia to *Cheiraster,* which is enlarged by inclusion in it of *Luidiaster* Studer as a subgenus. Two further subgenera of *Cheiraster* are described, *Barbadosaster* for *Cheiraster echinulatus* (Perrier) and *Christopheraster* for *C. mirabilis* (Perrier), also including *C. blakei* sp. nov. and two other species. On the basis of older collections and new material, mainly from the *Pillsbury* and *Gerda* collections of the University of Miami, the morphological and geographical ranges of certain species of these two genera and of *Benthopecten* are extended and several names are put in synonymy, tabular keys to the Atlantic species are also included.

Introduction

In the course of a major review of the Atlantic species of Asteroidea, assessment of the neglected deep-sea family Benthopectinidae proved so complicated as to necessitate a preliminary paper to dispose of some of the more complicated taxonomic problems.

The ordinal position of the Benthopectinidae will be discussed in the main study on Atlantic asteroids (Clark & Downey). The family was removed from the Paxillosida to the revived order Notomyotida Ludwig, 1910 by McKnight (1975).

Systematic discussion

Family **BENTHOPECTINIDAE** Verrill, 1894

Archasteridae Benthopectininae Verrill, 1894 : 245–246, 268.
Archasteridae Pontasterinae Verrill, 1894 : 246–247, 268.
Benthopectinidae Verrill, 1899 : 200, 217; Ludwig, 1910 : 442, 458–461; Fisher, 1911 : 120–122; Verrill, 1914 : 310–311; Spencer & Wright, 1966 : U48.
Plutonasteridae Pontasterinae Verrill, 1899 : 200.
Cheirasteridae Ludwig, 1910 : 442, 444–447.

Bull. Br. Mus. nat. Hist. (Zool.) **41** (3) : 91–135 Issued 29 October 1981

Name	Range	Conclusions
Acontiaster bandanus Döderlein, 1921	East Indies, 304 m.	
Benthopecten Verrill, 1884		
B. acanthonotus Fisher, 1905	California, 1800–1940 m.	
B. chardyi Sibuet, 1975	SE Atlantic, 2580 m.	Subsp. of *B. simplex* (Perr.)
B. claviger Fisher, 1910	Bering Sea—Oregon, 1800–1950 m.	
B. cognatus Ludwig, 1905	Gulf of Panama, 3030 m.	
B. fischeri (Perrier, 1894)	NW Africa, 1060–1430 m.	
B. folini (Perrier, 1885)	NW Africa, 2320–2330 m.	Dates only from 1894
B. heteracanthus Macan, 1938	Gulf of Aden, 2310 m.	
B. huddlestoni (Alcock, 1893)	Bay of Bengal, 2780 m.	
B. incertus Ludwig, 1910	'Indian Ocean'	
B. indicus (Koehler, 1909)	S of Sri Lanka, 830–1080 m.	
B. moluccanus Fisher, 1913	East Indies, 760 m.	
B. munidae H. E. S. Clark, 1969	S New Zealand, 740 m.	
B. mutabilis Fisher, 1910	British Columbia, 2870 m.	?To *Gaussaster*
B. pectinifer (Ludwig, 1905)	Galapagos—California, 1570–2320 m.	
B. pedicifer (Sladen, 1889)	Southern Ocean, 2930–3480 m.	
B. pentacanthus Fell, 1958	New Zealand, 730 m.	
B. pikei H. E. S. Clark, 1969	New Zealand, 550–630 m.	
B. pikei var. *australis* H.E.S.C., 1970	New Zealand, 1650–1690 m.	
B. polyctenius Fisher, 1913	East Indies, 1470 m.	
B. rhopalophorus Djakonov, 1950	Okhotsk Sea, 420 m.	
B. semisquamatus (Sladen, 1889)	Japan, 1030–3430 m.	See p. 95
B. semisquamatus celebensis Döderlein, 1921	East Indies, 920–1890 m.	
B. simplex (Perrier, 1881)	North Atlantic, 2000–2740 m.	
B. spinosissimus (Sladen, 1889)	Ascension I., 780 m.	
B. spinosus Verrill, 1884	E of U.S.A., 1300–3700 m.	
B. spinuliger (Ludwig, 1905)	Galapagos—Panama, 1620–2320 m.	
B. styracius Fisher, 1913	Philippines, 1650 m.	
B. violaceus (Alcock, 1893)	Laccadive Sea, 2190 m.	
Cheiraster Studer, 1883		
C. coronatus (Perrier, 1884)	West Indies, 340–380 m.	Syn. of *C. mirabilis*
C. diomedeae Fisher, 1917	Philippines, 770 m.	
C. echinulatus (Perrier, 1875)	West Indies, 100–300 m.	To subgen. *Barbadosaster* nov.
C. enoplus Verrill, 1915	West Indies, 750–840 m.	Syn. of *C. mirabilis*
C. gazellae Studer, 1883	Philippines—East Indies, 360–470 m.	
C. granulatus Ludwig, 1910	'Indian Ocean'	
C. inops Fisher, 1906	Hawaiian Is—Sri Lanka, 430–1250 m.	

C. ludwigi Fisher, 1913	East Indies, 1270 m.	
C. mirabilis (Perrier, 1881)	West Indies, 300–900 m.	To subgen. *Christopheraster* nov.
C. monopedicellaris McKnight, 1973	New Zealand, 720–770 m.	
C. niasicus Ludwig, 1910	Philippines, East Indies, 490–930 m.	
C. otagoensis McKnight, 1973	New Zealand, 720–1090 m.	
C. pedicellaris Studer, 1883	NE Australia, 1000 m.	
C. pilosus (Alcock, 1893)	S India, 1080–1310 m.	
C. richardsoni Fell, 1958	New Zealand, 730 m.	
C. snyderi Fisher, 1906	Hawaiian Is—Nicobar Is, 420–1670 m.	
C. subtuberculatus (Sladen, 1889)	SE Australia, 1740 m.	
C. triplacanthus Fisher, 1913	East Indies—SE Africa, 1050–1280 m.	
C. trullipes (Sladen, 1889)	Philippines, 1920 m.	
C. weberi Döderlein, 1921	East Indies, 470 m.	
C. yodomiensis Goto, 1914	Japan, 160 m.	?To *Nearchaster*
Gaussaster antarcticus (Sladen, 1889)	Southern Ocean, 2730–3060 m.	
Luidiaster Studer, 1884		Subgen. of *Cheiraster*
L. antarcticus (Koehler, 1907)	Southern Ocean, 3250 m.	
L. dawsoni (Verrill, 1880)	Bering Sea—W Canada, 100–290 m.	
L. dubius H. L. Clark, 1941	West Indies, 485 m.	Syn. of *Cheiraster sepitus*
L. gerlachei (Ludwig, 1903)	Southern Ocean, 160–810 m.	
L. hirsutus Studer, 1884	Southern Ocean, South Africa, 240–550 m.	
L. horridus (Fisher, 1906)	Hawaiian Is, 260–330 m.	To *Cheiraster (Christopheraster)*
L. oxyacanthus (Sladen, 1889)	Japan, 630 m.	To *Cheiraster (Christopheraster)*
L. planeta (Sladen, 1889)	S Chile—Falklands & Argentina, 350–500 m.	
L. teres (Sladen, 1889)	East Indies, 260 m.	
L. tuberculatus Djakonov, 1929	Japan Sea, 140–850 m.	
Myonotus intermedius (Fisher, 1910)	California, 1380–1750 m.	
Nearchaster Fisher, 1911		
N. aciculosus (Fisher, 1910)	Alaska—California, 550–1460 m.	
N. fisheri Döderlein, 1921	East Indies, 830–1020 m.	
N. pedicellaris (Fisher, 1910)	Alaska, 510 m.	
N. variabilis (Fisher, 1910)	Bering Sea—Alaska, 200–640 m.	
N. variabilis geminus Djakonov, 1950	Okhotsk Sea, 500–520 m.	
Pectinaster Perrier, 1885		
P. agassizi (Ludwig, 1905)	Galapagos—California and Gulf of Aden, 790–2320 m.	
P. agassizi evoplus (Fisher, 1910)	S California, 1800–1940 m.	
P. agassizi granuliferus Macan, 1938	Gulf of Aden, 2000 m.	
P. cribellum (Alcock, 1893)	Laccadive Sea, 2190 m.	to *Cheiraster*
P. dispar Verrill, 1915	West Indies	
P. filholi Perrier, 1885	NW Africa—NE America, 1200–3100 m.	

Name	Range	Conclusions
P. gracilis Verrill, 1915	West Indies, 130–550 m.	Syn. of *Cheiraster planus*
P. hispidus (Alcock & Wood-Mason, 1891)	Arabian Sea—Laccadive Sea, 880–2470 m.	Syn. of *P. mimicus*
P. mimicus (Sladen, 1889)	Laccadive Sea—New Zealand, 690–1690 m.	
P. mimicus hylacanthus Fisher, 1913	Philippines—East Indies, 700–800 m.	
P. mimicus malayanus Döderlein, 1921	East Indies, 1020–1910 m.	
P. mimicus palawanensis Fisher, 1919	Philippines, 1330 m.	
P. mixtus Verrill, 1915	West Indies, 130–1830 m.	Syn. of *C. echinulatus*
P. oligoporus (Perrier, 1894)	West Indies, 275 m.	Syn. of *C. echinulatus*
P. pristinus (Sladen, 1889)	Uruguay, 4840 m.	Syn. of *P. filholi*
P. robustus A. H. Clark, 1917	Chile, 2410 m.	to *C. (Luidiaster)*
P. vincenti (Perrier, 1894)	West Indies, 170 m.	Syn. of *C. echinulatus*
Pontaster Sladen, 1885		
P. sepitus (Verrill, 1885)	NE America, 670–1570 m.	to *Cheiraster*
P. tenuispinus (Düben & Koren, 1846)	Arctic—C. Cod, Bay of Biscay, 20–2000 m.	
Saraster insignis A. H. Clark, 1916	Lower California, 840 m.	Syn. of *Nearchaster insignis*

This family of primarily deep-water Asteroidea is in need of review, the last comprehensive survey being by Ludwig (1910), intended only as a preliminary treatment, modified by Fisher (1911), while Macan (1938) simply listed the species of *Pectinaster* and *Benthopecten* (the genera represented in the Murray Expedition collections), summarizing earlier conclusions about these two genera.

Since the present study concentrates on the Atlantic fauna, the genera *Acontiaster, Myonotus* and *Nearchaster*—known only from the Indo-Pacific—have not merited attention here but are listed below with the other taxa currently recognized together with nomenclatural modifications now proposed. *Saraster* A. H. Clark, 1916, type and only species, *S. insignis* A. H. Clark, is now synonymized with *Nearchaster.* It was described without comparative remarks or figures and the holotype (from Lower California) has disintegrated but the description leaves no doubt in my mind that it was conspecific with *N. aciculosus* (Fisher, 1910), taken at 14 *Albatross* stations off California (and further north), any differences being accountable to the smaller size of the type.

Additionally, the following names formerly reduced to synonyms are now otherwise disposed:

Benthopecten armatus (Sladen, 1889), NE America—Portugal, 2290–2470 m., synonymized with *B. spinosus* Verrill by Macan, 1938, following Verrill, 1899 and Grieg, 1921, treated as valid by Farran, 1913 and Mortensen, 1927 but now synonymized with *B. simplex* (Perrier), following Ludwig, 1910.

B. fischeri Perrier, 1894. NW Africa, 1060–1430 m, synonymized with *B. spinosus* by Macan, 1938, following Grieg, 1921, but now provisionally treated as valid or a possible synonym of *B. simplex.*

Cheiraster planus Verrill, 1915, West Indies (no details), synonymized with *C. mirabilis* (Perrier) by Downey, 1973, but now considered as valid.

Pontaster perplexus Perrier, 1894, NW Africa, 2320–2330 m., synonymized with *P. tenuispinus* (Düben & Koren) by Ludwig, 1910, but now synonymized with *Pontaster sepitus* Verrill, which is itself now revived from the synonymy of *(C.) echinulatus* (Perrier), to which it was referred by Ludwig, 1910, and newly referred to *Cheiraster.*

Pontaster venustus Sladen, 1889, Azores—Portugal, 1250–4000 m., with var. *robusta* Sladen, 1889, Cape Verde Is area, depth ?, synonymized with *Pectinaster filholi* Perrier by Macan, 1938, following Ludwig, 1910, but now synonymized with *Cheiraster sepitus.*

B. semisquamatus (Sladen, 1889) was treated by Goto, 1914, without explanation as a synonym of *B. spinosus* Verrill, apparently extending Verrill's synonymy of *B. semisquamatus* var. *occidentalis* to the Pacific *semisquamatus* itself, despite Ludwig's retention in 1910 of this as valid, followed by Fisher (1919 : 210) and Döderlein (1921). Okutani (1969) has followed Goto.

The genera of Benthopectinidae can be distinguished by the tabular key (Table 1).

Some of the generic limits within the Benthopectinidae are still ill-defined. In Ludwig's review (1910), on the strength of the unusual dorsal arm muscles, the present family was interpreted as a suborder Notomyota including two families: Cheirasteridae (for *Cheiraster* Studer, 1883, *Luidiaster* Studer, 1884, *Pontaster* Sladen, 1885 restricted, *Pectinaster* Perrier, 1885, *Marcelaster* Koehler, 1907 and *Gaussaster* nov., of which *Marcelaster* was synonymized with *Luidiaster* by Fisher, 1940) and Benthopectinidae (for *Benthopecten* Verrill, 1884 and *Pararchaster* Sladen, 1885). The latter group was distinguished by the presence of odd interradial marginal plates, the superomarginal ones with unusually large spines.

Fisher (1911) described two new genera, *Nearchaster* and *Myonotus*, both with the

Table 1 Tabular key to the genera of Benthopectinidae. Entries in brackets indicate a slight development or tendency.

	1	2	3	4	5	6	7	8	9
Benthopecten	A	w/b	L	f	M/R	+	2 (3)	p	F
Myonotus	A	w/b	L	p	M	+	2	p	F
Nearchaster	I	w	L	p	M	+	2 (3)	p	F
Gaussaster	I	b	L	f	R (M)	+	3,2	p	F
Acontiaster	R	w	D	p	M	(+)	2	u	F
Cheiraster (*Luidiaster*)	R	b (w)	L	p	M	−(+)	2	p	F
Cheiraster (*Barbadosaster*)	R	b	D	f (p)	M	−	2 (3)	p	F
Cheiraster (*Christopheraster*)	R	d	D	p (f)	M	+	1 (2)	p	F
Cheiraster (*Cheiraster*)	R	b	D	p	M	−	1	p	F
Pectinaster	R	o	L	p	M/R	−	1	p	F
Pontaster	R	o	L (D)	p	M	−	2,3	p	B

1. Interradial suture between the marginal plates:
   A–absent, an odd plate present in each series, the superomarginal one inset on to the disc
   I–often irregular, plates asymmetric or odd plates in some or all interradii but the superomarginal one on the periphery of the disc
   R–regular, no odd interradial plates (though the sutures are occasionally asymmetric in one or two interradii)

2. Papular areas:
   b–bilobed distally (except in small specimens, R < 30 mm), limited to the arm bases, initiated from a single median proximal primary pore
   d–initially double, two lateral areas on each arm base merging proximally in large specimens, R > 80 mm, to form a bilobed area, pores relatively small and interstitial
   o–oval and swollen with deepened plates forming well-defined median papularia
   w–widespread over most of disc and at least the proximal parts of the arms

3. Superomarginal plate alignment:
   D–partly or mainly dorsal, framing the paxillar area in dorsal view
   L–mainly lateral, inconspicuous dorsally

4. Abactinal plates of disc and arm bases:
   f–flat, usually scale like, with only a small median elevation, if anything
   p–(para-)paxilliform with a more or less well defined median column or convexity

5. Armament of most abactinal plates:
   M–multiple, with a cluster of spinules, often surrounding a larger median spinelet or spine, sometimes totally lacking
   R–reduced, often to a single spinule or spinelet throughout

6. Central armament of primary and some other proximal plates
   +–large spines 2+ mm long present
   −–only 1 (rarely 2,3) central spinelets of larger plates enlarged up to *c.* 1·5 mm

7. Subambulacral spine number

8. Dorsal arm muscles:
   p–paired, attached proximally to one or two ambulacral plates and the adjacent marginals, or to the abactinal body wall, or both
   u–united in a single mass, attached proximally only to the body wall

9. Pedicellariae (if present):
   B–bivalved with only two elongated valves, on adambulacral plates only
   F–fasciculate with multiple narrow tapering valves, usually in two, occasionally three, combs on adjacent plates (pectinate), usually present on actinal plates, sometimes on abactinal and marginal plates, occasionally lacking.

interradial marginals more or less irregular in position, so that one plate of each series is often more or less mid-interradial but the armament of such odd superomarginals is not conspicuous. Inevitably, such intermediate taxa prompted him to amalgamate the Cheirasteridae with the Benthopectinidae. Apart from synonymizing *Pararchaster* with *Benthopecten,* he accepted the genera cited by Ludwig.

Among the genera with no odd interradial marginals, Fisher distinguished *Pontaster* and *Pectinaster* with 'entire and swollen' papularia from *Cheiraster* and *Luidiaster* with 'flat and two-lobed' papular areas, separating *Pontaster* from *Pectinaster* on the presence of bivalved rather than fasciculate pedicellariae and *Cheiraster* from *Luidiaster* on the single rather than multiple subambulacral spines—the only difference evident from a comparison of Ludwig's diagnoses. To supplement these criteria, Fisher proposed to use the proximal attachment of the dorsal arm muscles—to one or two ambulacral plates and the two adjacent marginals in *Luidiaster* but to the dorsal body wall and the superomarginals in *Cheiraster.* However, in 1919 he had to modify this after finding that the type-species of *Cheiraster, C. gazellae* Studer, does have tendons to the twelfth and thirteenth ambulacral plates, though inconspicuous ones, and these plates lack the enlarged crests of the comparable plates of *L. hirsutus,* the type species of *Luidiaster*, and even more *L. dawsoni.* I find that *L. hirsutus* additionally has the attenuated proximal ends of the muscles attached to the dorsal body wall just distal to the V-shaped area defined by the two lobes of the papular area, as well as having a tendon to a laterally swollen crest of an ambulacral plate (the sixth plate in a specimen with R 85 mm). Fisher himself (1940) found a much stouter link between the main part of the muscle and the dorsal body wall in the *Discovery* specimen of *Pontaster planeta* Sladen, a species later referred to *Luidiaster* (A.M.C., 1962) on account of the V-shaped flat papular areas and multiple subambulacral spines, and closely related to *L. hirsutus.* The muscle appears to me to extend nearly to the seventh ambulacral, ending opposite the fourth superomarginal, the distalmost papular pores being just proximal to this (as in *L. hirsutus*), although Fisher described it as ending level with the ninth ambulacral. He also noted a 'rudimentary' tendon to the eighth ambulacral in *planeta.* In *Cheiraster mirabilis* (Perrier), which has abruptly enlarged fourth superomarginal plates, I find that there is a stout tendon to this marginal and the adjoining seventh ambulacral but no connection to the dorsal body wall.

Clearly, the muscle attachment shows too great a range in these various species for use as a character of generic weight. This leaves only the number of subambulacral spines to distinguish between *Cheiraster* and *Luidiaster* but I think that the alignment of the superomarginal plates is also of more than specific significance. Hitherto, this alignment has not been regarded as important, possibly because of the considerable range of form in the very variable species *Pontaster tenuispinus*, so that Ludwig suggested synonymy of *Pontaster venustus* with dorsally broad superomarginals with *Pectinaster filholi* where the marginals are almost entirely lateral. However, limitation of *Pectinaster* to species with laterally aligned superomarginals results in a much more natural grouping, since such species also have specialized compact papularia, those with dorsally broad superomarginals having much more diffuse pore areas potentially or actually bilobed in form with the abactinal plates within the areas little modified (compare Figs 1a & b). Verrill (1915 : 137) discounts the importance of the subambulacral spine number in ascribing the specimen he named *enoplus* to *Cheiraster* despite the two large subambulacral spines of the large holotype (R 185 mm). Study of a good size range of *C. mirabilis* now shows that doubling of the subambulacral spine number is common in very large specimens, R > 120 mm, and that *C. enoplus* Verrill is a synonym, the holotype sharing the very distinctive abrupt enlargement of the fourth superomarginal plates and spines.

With regard to the Atlantic species of Benthopectinidae, no less than 18 other nominal species which have been included in *Pontaster, Pectinaster, Cheiraster* and *Luidiaster* need to be taken into consideration, namely (in chronological order):

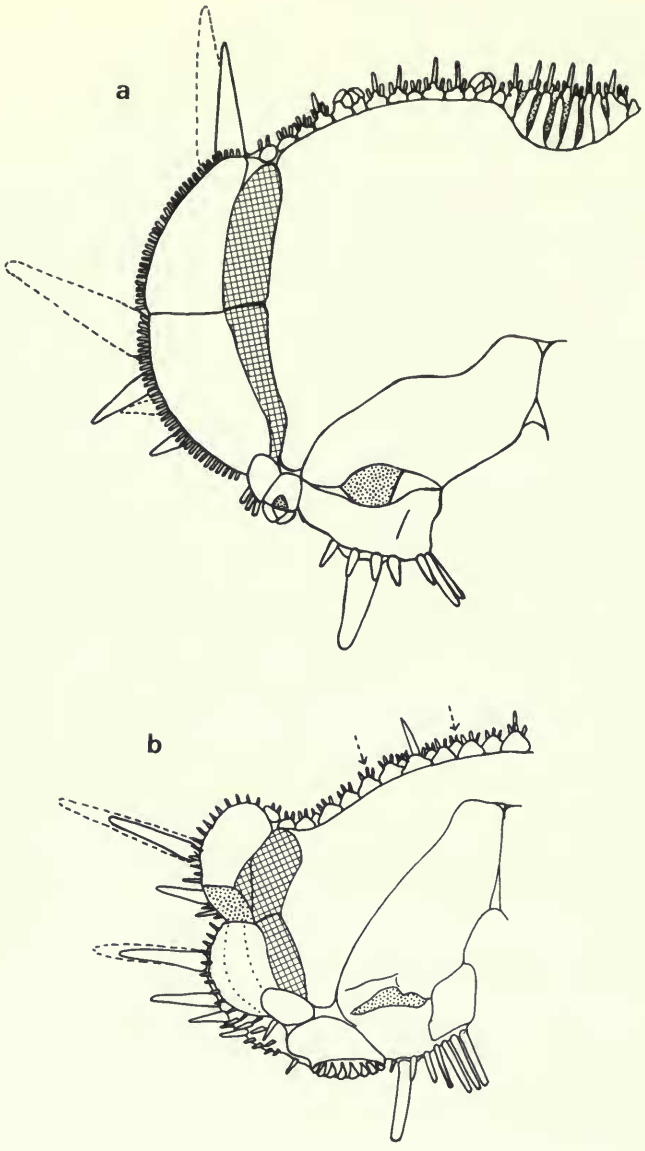


Fig. 1 Half sections through the base of a ray bisecting the papularium or papular area, showing the armament of the second supero- and inferomarginal plates with their proximal and internal (hatched) faces, the fully developed spines of the third plates shown by discontinuous lines. (a) *Pectinaster filholi* Perrier, syntype of *Pontaster forcipatus* Sladen, *Challenger* st. 44, 45 or 50, BMNH no. 90.5.7.50(pt), R *c.*75 mm; (b) *Cheiraster (Christopheraster) blakei* sp. nov. *Oregon* st. 4294. R. *c.* 70 mm. [In (b) the vertical faces of the two marginals are not in the same plane; the position of the lobe of the papular area is indicated by the arrows.]

Pontaster tenuispinus (Düben & Koren, 1846)	NE Atlantic, Arctic
Cheiraster echinulatus (Perrier, 1875)	West Indies
C. mirabilis (Perrier, 1881)	West Indies
Luidiaster hirsutus Studer, 1883	Kerguelen, South Africa
C. coronatus (Perrier, 1884)	West Indies
Pontaster sepitus (Verrill, 1885)	NW Atlantic
Pectinaster filholi Perrier, 1885	NE Atlantic
Pontaster venustus Sladen, 1889	Azores, Cape Verde area
Pectinaster pristinus (Sladen, 1889)	SW Atlantic
Luidiaster planeta (Sladen, 1889)	E & W Patagonia, Falklands
Pectinaster vincenti (Perrier, 1894)	West Indies
Pontaster perplexus Perrier, 1894	West Indies
Pectinaster oligoporus (Perrier, 1894)	West Indies
P. dispar Verrill, 1915	West Indies
P. gracilis Verrill, 1915	West Indies
P. mixtus Verrill, 1915	West Indies
C. planus Verrill, 1915	West Indies
Luidiaster dubius H. L. Clark, 1941	West Indies

Of these, *Pontaster venustus* was synonymized with *Pectinaster filholi* by Ludwig (1910), followed by Macan (1938) but is now found to be referable to *Cheiraster* because of its irregular bilobed papular areas and dorsally broad superomarginal plates. The oval, well-defined papularia of *P. filholi* are constructed of much deeper plates than the other abactinal ones, laterally grooved to accommodate the papulae (Fig. 1a). The same combination of less compact actually or potentially bilobed papular areas and relatively broad superomarginals as in *P. venustus* is also shown by the types of *Pontaster sepitus, Pectinaster vincenti, Pontaster perplexus, Pectinaster oligoporus, Pectinaster dispar, Pectinaster gracilis* and *Pectinaster mixtus,* all of which have been examined. These encompass a size range of R 26–*c.* 55 mm.

Pectinaster pristinus is known only from a single small specimen, R *c.* 18 mm, from off the River Plate. This was in poor condition, the abactinal plates obscured by mud; when this was removed, no significant difference could be seen in the armament from specimens of *P. filholi* of similar small size from the North Atlantic.

Accordingly, both *Pontaster* and *Pectinaster* are reduced in the Atlantic to single species (indeed *Pontaster* is a monotypic genus).

Following study of many benthopectinids from the U.S. National Museum and M.C.Z., Harvard collections, together with the *Pillsbury* and *Gerda* material of the University of Miami from the tropical Atlantic, I consider that most of the 16 remaining names listed above (which fall within the scope of *Cheiraster* and *Luidiaster*) are synonyms, only five being for valid species. This superfluity of names arose mainly from Perrier's confused treatment of the *Blake* collections (1881 and 1884 with afterthoughts in 1894), which was partly resolved but further complicated by Verrill's failure to take growth changes into account in his review of 1915.

One character of limited use is the R/r ratio, which tends to increase with the absolute size, so that species such as *C. mirabilis,* which may exceed R 120 mm, may achieve an R/r ratio of as high as 9/1, from usually 7–8/1 at R *c.* 100 mm or only *c.* 5/1 at R 20 mm. However, in *C. sepitus* with a maximum R of probably 70 mm, the ratio stays near 5/1 in specimens larger than R *c.* 30 mm.

Since individual papulae do not appear to increase disproportionately in size with growth of the whole animal, their number must increase in order to maintain adequate respiratory function. In most of the species under discussion the first (primary) pore usually appears at R 10–15 mm near the base of each arm distal to the primary radial plate, which at this small size is usually still distinguishable among the other disc plates; further pores, usually smaller, are added progressively around it, especially distally and laterally. Only *Cheiraster mirabilis* and *C. coronatus* (sensu H. L. Clark, 1941) differ from the rest in developing not one primary

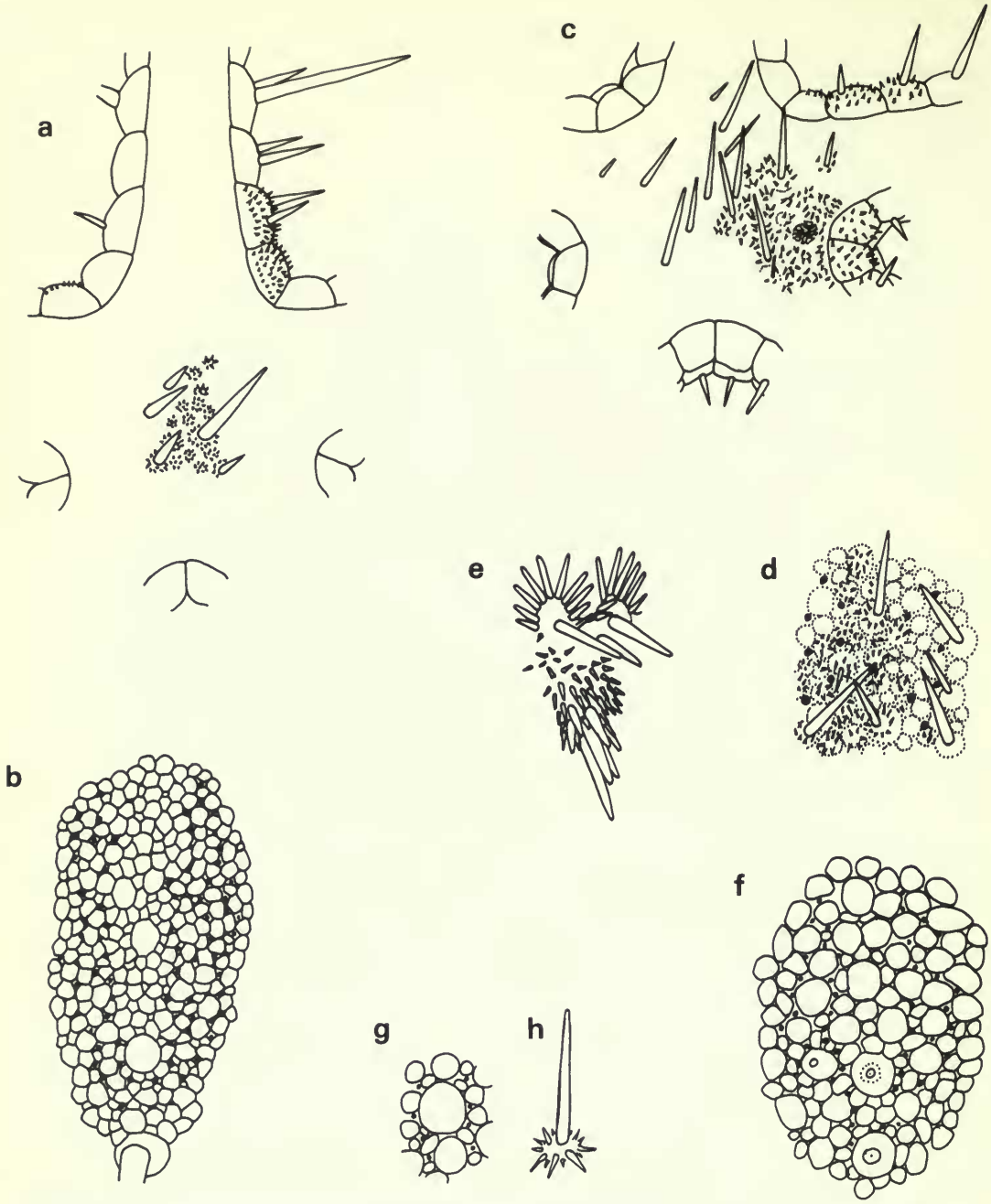
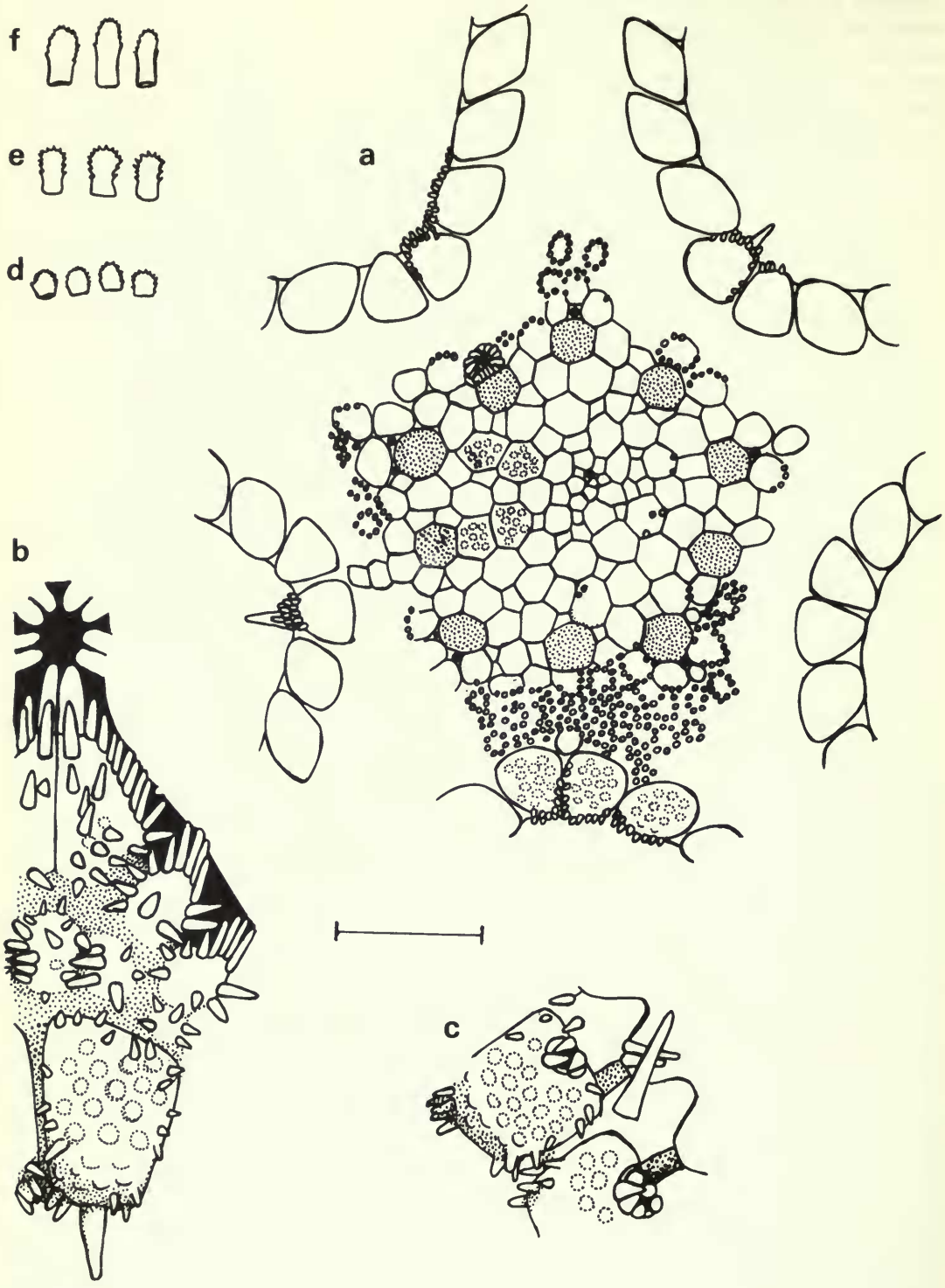


Fig. 2 (a and b) *Cheiraster (Christopheraster) mirabilis* (Perrier). (a) *Atlantis* st. 3444, 3445, 3447 or 3449, MCZ 3912(pt), R 25 mm, to show disc and proximal marginal spines; (b) Holotype, *Blake* st. 148, MCZ 10, R 87 mm, papular area (the proximal end lowermost); (c–f) *Cheiraster (Christopheraster) blakei* sp. nov. (c) *Atlantis* st. 3444, 3445, 3447 or 3449, MCZ 3912(pt), R 21 mm, for comparison with (a); (d) *Atlantis* st. 2963F, MCZ 3915, R 112 mm, part of intact papular area (most of the spines unnaturally appressed); (e) *Blake* st. 19, MCZ 2179, R *c.* 40 mm, second inferomarginal plate, adjoining actinal area and two adambulacral plates; (f) *Blake* st. 295, MCZ 216, R *c.* 45 mm, denuded papular area showing the spine sockets on two midradial plates, the upper one probably the primary radial; (g, h) *Cheiraster (Christopheraster) horridus* Fisher, holotype, *Albatross* st. 4079 (Hawaiian Is), USNM 21156, R 35 mm; (g) part of denuded papular area showing varied plate size and relatively small pores; (h) armanent of one large disc plate.

pore but a pair of smaller pores offset one each side of the primary radial plate; additional similarly small pores appear laterally and distally but few develop in the proximal mid-radial area, even at a large size, so that the two lateral pore areas only become loosely linked (Fig. 2b & f). At R >100 mm, the total pore number in these two species exceeds 100 on each ray, far more than in the other species of *Cheiraster* with their larger papulae, so that for instance *C. planus* at R 100 mm has only *c.* 50 pores in each area. From the median primary pore these develop fairly regularly in this species in a curved double row on each side, forming a horseshoe-shape; only at R >70 mm do the added pores form a more irregular and elongated area (Fig. 5). The early stages of this sequence are shown by the illustrated holotype and paratype of *Pectinaster gracilis* (Verrill, 1915, pl. 6, fig. 1 & pl. 15, fig. 1b); the smaller paratype (R probably *c.* 20 mm) has only three pores in a transverse line, the median one enlarged, while the holotype (pl. 6) at R 30 mm usually has just two additional pores placed distal to the lateral ones forming a very shallow U. Although not stated by Verrill, the holotype has most superomarginal spines distinctly longer and stouter than the corresponding inferomarginal spines—a characteristic of *C. planus*—as well as compact parapaxillae, uniformly short inferomarginal spinules giving a smooth contour to the plate (apart from the main and accessory spines), large single subambulacral spines and relatively blunt-angled furrow margins to the adambulacral plates. Consequently, *P. gracilis* should be treated as a synonym of *C. planus.*

A similar sequence in the early development of pores is shown in *Cheiraster echinulatus, Pectinaster vincenti* and *P. mixtus,* also in *Pontaster sepitus, P. venustus, P. perplexus, Pectinaster oligoporus* and *P. dispar* (and almost certainly occurred in the holotype and only recorded specimen of *Luidiaster dubius* before it reached its final size of R *c.* 60 mm). In these, however, the later developed pores are more irregular in position than those of *C. planus,* forming at first a square or transverse patch (Fig. 4b) and then an elongated bilobed area, often asymmetrically so or with the distal pores of the two lobes approximating medially (as in the holotype of *P. vincenti,* Fig. 4g) to form an almost oval area. The maximum R in these nominal species does not appear to exceed 70 mm and the pore number 36. Most specimens taken are in the R 20–40 mm range. (Genital pores first appear in *Cheiraster* at R 10–15 mm close to the first superomarginal plates.)

The holotypes of *C. echinulatus, mixtus* and *vincenti* have R 16 mm, 26 mm and 42 mm and the pore number in each area is 1–3, 3–5 and *c.* 12 respectively, an increase compatible with the size differences. All show the following characters: the abactinal plates are very mixed in size, polygonal, abutting fairly closely together, distinctly flattened in the two smaller specimens but somewhat convex in the larger one, especially on the papular areas, armed with numerous (up to *c.* 30) short 'spinules' of superficially granuliform shape (though with height/breadth >2/1 in the largest) arising from most of the surface of the plate and encircling in a double ring on many plates a slender needle-like spinelet; the superomarginal plates are broad in dorsal view, the two opposite ones together taking up *c.* 50% of the total arm breadth; the marginal spines are relatively slender, most inferomarginal ones longer than the corresponding superomarginal spines, while several of the inferomarginal spinules below the spine are more or less enlarged into accessory spinelets so as to give a rough profile to the body; the furrow margins of the proximal adambulacral plates form an acute angle prolonged into the furrow (the distal plates being truncated) and the subambulacral spines are multiple (except perhaps in the small holotype of *C. echinulatus* where Perrier described a complete circle of 10–12 peripheral spines (including those projecting over the furrow, around a larger central spine but all the subambulacral spines are now [1980] lost or displaced). The coincidence of all these characters is convincing evidence that the three are conspecific, so that *Cheiraster vincenti* and *Pectinaster mixtus* become synonyms of *C. echinulatus.* The type localities of *C. echinulatus* and *vincenti* are near the neighbouring Lesser Antillean islands of Barbados and St Vincent; that of *mixtus* is off Havana, Cuba (Verrill's 'West of Florida' deriving from a misreading of the coordinates for *Albatross* st. 2341). Many other specimens from intermediate and western caribbean localities to a confirmed depth of 567 metres show variation not only in the convexity of the


f
e
d
a
b
c

abactinal plates and arrangement of the pores but also in the size of the pores, which reach a maximum number of 36 in a specimen with R 65 mm. The frequency of pedicellariae, as usual, is rather variable; there are some pectinate actinal ones is *c.* 50% of specimens but only *c.* 5% (including the holotypes of *C. echinulatus* and *mixtus*) have a few fasciculate inferomarginal pedicellariae adjoining the adambulacrals. The holotype of *P. oligoporus* from the Leeward Is. in 275 m is in very poor condition but its flattened abactinal plates and the prolonged furrow angles of the adambulacrals show that it too is conspecific with and a synonym of *C. echinulatus.*

For the rest, the type localities of *C. sepitus, venustus* (with var. *robusta*), *perplexus, dispar* and *dubius* are scattered all over the North Atlantic, respectively: S of Cape Sable, Nova Scotia, 1570 metres, the Azores, 1650 metres (Cape Verde Islands, depth unknown), off Cap Blanc, W. Africa, *c.* 2325 metres, the Leeward Is, 1260 metres and S of Cuba, 485 metres. (For *Pectinaster dispar* Verrill cited the source as an *Albatross* station, locality unknown, but the labels now with the specimen indicate st. 2751, which is 16° 54′ N, 63° 12′ W.) The relevant type specimens have R measurements and pore numbers as shown in table 2.

Table 2

Name	*sepitus*	*venustus*	v. *robusta*	*perplexus*	*dispar*	*dubius*
R (mm)	37	37	46	52	35 + (?45–50)	*c.* 63
Pores	15	7–9	8	21	10–13	11–14

The figures for C. sepitus are from what may be called a 'topotype' in the USNM, no. 24525, since the two syntypes (from *Albatross* st. 2072) are now in a state of disintegration and were never properly described by Verrill. This specimen was named *P. sepitus* in Verrill's hand and was from a station (2075) with almost identical coordinates and depth.

Although sharing with *C. echinulatus* the dorsally broad superomarginal plates taking up 50% or more of the arm breadth, these all differ from that species in several features. The abactinal plates are more loosely joined and consistently markedly convex and parapaxilliform, with more elongate and somewhat pointed spinules usually numbering only 5–15, clustered together on the central (highest) part of the plate, though again often surrounding a central spinelet several times longer; the superomarginal plates, though with a similar mean breadth to those of *C. echinulatus,* are somewhat longer and often more convex, numbering only *c.* 16 at R 20 mm or *c.* 27 at R 50 mm, compared with *c.* 20 and *c.* 30 at the same sizes in *echinulatus*; the marginal spines are shorter and much stouter basally, being conical in shape, though again the inferomarginal spines tend to be longer than the superomarginal ones and the upper inferomarginal spinules are likewise more or less elongated; the subambulacral spines are usually single, stout-based and conical (as usual in all these species similar in form to the marginal spines) and pedicellariae are rarely present at all, even on the actinal plates they were only found in less than 10% of specimens. Possibly in larger specimens, R > 50 mm, the arms remain relatively shorter than in *C. echinulatus*, R/r not much exceeding 5·0/1 where *echinulatus* may reach 6/1, but this remains to be seen from

Fig. 3 *Cheiraster (Barbadosaster) echinulatus* (Perrier) (a) Holotype, *Hassler,* Barbados, Paris Museum (PM) 3481, R 16 mm, disc and arm bases from above, the primary radial and interradial plates stippled, crystal bodies indicated on a few larger abactinal and marginal plates (the centre of the disc rubbed almost bare of spinules); (b, c) the same, part of a ventral interradius and the fourth and fifth adambulacrals with adjacent inferomarginal plates, most armament lost, the subambulacral spine drawn on the fifth plate appressed; (d–f) abactinal spinules of: (d) the holotype of *C. echinulatus,* (e) holotype of *Pectinaster mixtus* Verrill, R 26 mm and (f) specimen from *Gerda* st. 628, R 66 mm. The scale equals 2 mm for (a), 1 mm for (b) and (c) and *c.* 0·5 mm for (d)–(f).

further intact specimens. (Perrier's implication that there is more than one subambulacral spine in the holotype of *perplexus* is not borne out by re-examination. It may also be noted that he gave the pore number as 'une quinzaine' but removal of the spinelets in one area revealed the higher number of 21. Verrill's estimate for the type of *dispar* was also too low).

With all these features in common, I do not think that the wide spread of pore numbers from 21 at R 52 in the type of *perplexus* to only 8 in that of the geographically close *venustus* var. *robusta* at R 46 mm is significant. The 'topotype' of *sepitus* has as many as 15 at R <40 mm. Other similar specimens, with R 19–46 mm collected at five *Pillsbury* stations off Venezuela and two *Discovery* ones from the Azores, all of which I consider are conspecific with *C. sepitus,* have 0–12 pores in individual areas, often with a range of three or more in different radii of the same specimen, one with R 41 mm having from 6 to 12 pores in the five radii. Consequently, *P. venustus, perplexus, dispar* and *L. dubius* are now referred to the synonymy of *C. sepitus,* the oldest name.

All the West Indian *Pillsbury* specimens now referred to *C. sepitus* are from depths greater than 1000 metres, as with the type locality of *P. dispar,* which casts doubt on the depth record of only 485 metres for the holotype of *L. dubius.*

A further nomenclatural problem remains to be resolved concerning the two species generally known as *C. mirabilis* and *C. coronatus,* at least sensu H. L. Clark, 1941.

In his preliminary account of the *Blake* asteroids, Perrier (1881) described *Archaster mirabilis* (stations unspecified) firstly (paragraphs 1–4) from a specimen with R/r given as 87/12 mm, only 6–10 spines around the anus and otherwise granulous abactinal plates; he then commented on another specimen with R/r 45/12 mm. In the full report (1884) the first specimen is redescribed at the beginning of the account of *A. mirabilis*, the station given as 148, St Kitts, and the second specimen is separated off as holotype of *Archaster insignis* (since referred to *Dytaster* in the Astropectinidae), as noted by Verrill (1915). Other specimens from 46 different stations were also included under the name *mirabilis* but the one with R 87 mm from st. 148 must be the holotype.

Also in 1884, Perrier described *Archaster coronatus* from a specimen with R 65 mm, R/r 8/1, citing stations 2 and 19. The sample from st. 19 is in the MCZ, Harvard, labelled as syntypes but the largest specimen is badly broken and its R probably did not exceed 40 mm, so, as Verrill (1915) assumed, the holotype must be from st. 2, off Havana, Cuba, and in the Paris Museum. In 1894, Perrier inadmissably redescribed the holotype of *mirabilis* (R/r slightly modified to 85/10) as '*C. coronatus* premier type', as Verrill (1915) noted when he repeated Perrier's 1884 description for *coronatus,* ranking it as a subspecies of *mirabilis.* H. L. Clark (1941) satisfactorily distinguished two West Indian species of *Cheiraster* with spines several mm long on the disc in the following terms:

mirabilis	*coronatus*
1. Paxillae very low and closely covered by a group of minute spiniform granules, none of which are enlarged or lengthened into spinules [spinelets in my terminology.]	1. Paxillae more convex with fewer and more unequal granules, one (or sometimes more) of them elongated into a spinule.
2. 3–10 relatively conspicuous spines 3–8 mm long at the centre of the disc.	2. Spines up to 3–4 mm long but never forming a conspicuous isolated group.
3. Fourth superomarginal spine up to 10–12 mm long.	3. Fourth spine up to 5 mm long.

After examining the *Blake* and *Atlantis* specimens in the MCZ and the *Gerda* and *Pillsbury* material I can add the following:

1a. Abactinal plates too low to be called 'paxilliform'; armed with up to *c.* 35 (mean number *c.* 15) short pointed spinules in compact groups.	1a. Armament of abactinal plates consisting of up to *c.* 25 (mean *c.* 10) distinctly elongated radiating spinules, the longer central spinelets graduated to the disc spines.

2a. The big disc spines closely clustered in the centre, not extending to the primary radial plate on the arm base; usually 5–15 spines, rarely >20.	2a. Big spines spaced, extending on to the papular areas in larger specimens and graduating to the central paxillar spinelets, usually >10 even at R only 30 mm, up to *c.* 75 at R 100 mm.
3a. Fourth (rarely the fifth) superomarginal plate and spine abruptly enlarged, the corresponding inferomarginal plate reduced and often spineless.	3a. In larger specimens the fifth or sixth marginal spines the largest and graduated to the adjacent spines.
4. Marginal plates covered with fairly uniform short pointed spinules, only a few on the lower face of the inferomarginals enlarged to spinelets; profile superficially smooth.	4. Several more or less elongated spinules/spinelets at the upper end of the inferomarginals giving a shaggy appearance and rough profile.
5. Furrow margins of adambulacral plates rounded or with obtuse angles.	5. Furrow margins 90° or acute, angles prolonged into the furrow.

Unfortunately, Perrier's 1884 description of *C. coronatus* described the abactinal armament as including *c.* 15 spines *around the anus* and the fourth superomarginal spine as *much larger than the others* (my italics). Although 15 disc spines is a high number for *C. mirabilis* at R 65 mm it is not unprecedented (see Table 4). Accordingly, it seems unavoidable that the name *coronatus* should be referred to the synonymy of *mirabilis*, as was done by Downey (1973), following Ludwig (1910), though evidently without appreciation of the existence of the two species recognized by H. L. Clark.

A new name is therefore needed for the species with less conspicuous, more numerous and graduated disc spines and graduated superomarginal spines. Although H. L. Clark has the credit for distinguishing the species, knowing his antipathy to the use of personal names I propose the name *C. blakei* after the ship which first collected it. As the MCZ specimens from *Blake* station 19 are in poor condition, a large specimen from *Gerda* st. 918 (between Florida and the Bahamas), described on p. 113 has been selected as holotype.

Turning to the species of *Luidiaster* (other than *L. dubius* disposed of above), the smallest specimen available of *L. hirsutus* from South Africa has R *c.* 35 mm (R/r 4·5/1) and *c.* 30 pores/area but a primary median pore is distinguishable, as in *Cheiraster* sensu stricto. The pore areas are V-shaped with mostly two rows of pores in each limb whereas larger specimens, R *c.*80 mm, have 110–160 pores in a more irregular but still bilobed area. The type series of *L. planeta* from Chile, R 26–37 mm, shows 9–14 pores and the primary ones are distinct. These two southern species, *L. hirsutus* and *L. planeta,* both have the superomarginals inconspicuous in dorsal view, aligned mainly on the sides of the arms, unlike the species of *Cheiraster.* They also have two or more large subambulacral spines (though at R 35 mm in *L. hirsutus* the two spines are more or less markedly unequal) and H. L. Clark (1926) found single spines in his smallest specimen, R 16 mm). However, the West Indian *Cheiraster echinulatus* has two or even three subambulacral spines from a small size, R. *c.* 20 mm, while large specimens of *C. mirabilis* and *C. blakei* (R >100 mm) often develop a second spine, though most individuals have only one on most plates. (Second spines usually appear first on the distal half of the arm and on the very first plate.) Although large specimens of *C. mirabilis* and *blakei* may have the superomarginal plates relatively narrow dorsally, they still form a small border to the paxillar area and in *C. echinulatus* they are consistently broad.

I doubt whether the alignment of the superomarginal plates unsupported is of sufficient weight to justify a generic distinction for *Luidiaster hirsutus* so that *Luidiaster* is now treated as a subgenus of *Cheiraster.* Both names were introduced by Studer, 1883, who separated them, and even referred *Luidiaster* to the Astropectinidae, because the specimens of *Cheiraster gazellae* had the dorsal body wall sufficiently transparent to show the underlying muscles, which he took for gonads. However, he failed to name a type species for *Luidiaster* until 1884, from which date only the name is valid.

The main characters by which the seven Atlantic species of *Cheiraster* can be distinguished are summarized in Table 3. (The number of adambulacral plates corresponding to the first ten inferomarginals does not seem to me to be significant in *Cheiraster*, though it may be useful for certain species of *Benthopecten*.) Synonymies and ranges for five of these species are given on pp. 112–8.

Table 3 Tabular key to the Atlantic species of *Cheiraster* sensu lato. Brackets signify occasional or partial conditions.

	1	2	3	4	5	6	7	8	9	10	11	12
blakei	6·0–8·5/1	20/27/33	M	c	D	e	I	g	(R)	1 (2)	AM (D)	*c.* 130
mirabilis	7·5–8·5	20/30/37	L	(f)	D	a	I	u	R	1 (2)	AM (D)	185
hirsutus	5·5–7·0	20/27/*c.* 35	A	c	PC	e	I	g	(P)	2,3 (1)	(A)	92
planeta	*c.* 5	20/35/?42	A	c	PC	e	I	g	R,* P	2,3 (1,4)	(A,D)	100
planus	6·0–7·0	18/25/30	A	c	PC	e	S	u	R	1	A (M)	*c.* 100
sepitus	4·5–5·5	16/25/30	A	c	PB	e	I	g	(P)	1	((A))†	*c.* 60
echinulatus	4·8–6·0	19/27/34	A	f	PB	e	I	g	P	2 (1–3)	A (M)	*c.* 70

**C. planeta.* In the type series from S Chile, the furrow margins are acute but not in the Falkland Is specimen.
†*C. sepitus*. Only five out of 60+ specimens examined have any actinal pedicellariae.

1. R/r at R 50+ mm.

2. Number of superomarginal plates at R 20, 40 and 60 mm (some obtained by extrapolation)

3. Disc spines:
   L–few and relatively very large, rarely > 15, restricted to centre of disc; no central paxillar spinelets graduating to the spines:
   M–moderately large centrally but not more than ½ r, spaced and often extending on to the papular areas, graduating in size down to the central paxillar spinelets
   A–absent, only central paxillar spinelets on many disc and mid-radial arm plates, not > 1·5 mm long

4. Proximal abactinal plates:
   c–convex, parapaxilliform, butting loosely together, spinules clustered on the raised area, mean no. 10–12 or less
   f–flat or low convex, polygonal, butting more or less closely together, spinules covering most of the surface and more numerous, mean no. 15–20

5. Papular areas:
   PB–initiating from a single large median primary pore, becoming irregularly bilobed, sometimes indistinctly so
   PC–initiating from a single large median primary pore, becoming crescentic (horseshoe-shaped), V-shaped or bilobed with long lobes
   D–double, initiating from a pair of pores, one each side of the mid-line, forming two diffuse lobes, merging proximally only in large specimens, R > 70 mm

6. Largest marginal spines:
   a–Fourth superomarginal spine abruptly and conspicuously enlarged, fourth inferomarginal plate reduced and often lacking a spine
   e–Marginal spines fairly even in size or the fourth to seventh (according to size, only the fourth in smaller specimens) enlarged but graduated

7. Marginal spines, relative length:
   I–most inferomarginal spines longer than the corresponding superomarginal ones
   S–most superomarginal spines longer (at least on the proximal half of the arm)

8. Inferomarginal spinules at the upper end of the plate:
   g–graduated, several becoming more or less elongated, graduating to the accessory spine(s) or spinelets, profile rough
   u–fairly uniform, only some enlarged spinelets on the lower face of the plates, profile fairly smooth between the spines

9. Furrow margins of adambulacral plates:
   P–with acute angles prolonged into the furrow, $<90°$
   R–rounded or with angles obtuse or right-angled

10. Subambulacral spine number

11. Pedicellariae:
   A–actinal
   M–marginal
   D–dorsal

12. Maximum recorded R

As a result of these comparisons between the Atlantic species, two further supraspecific groups can be recognized within the genus *Cheiraster.*

Firstly, the essentially dual nature and different ontogeny of the papular areas in *Cheiraster mirabilis* and *C. blakei* compared with the other species of *Cheiraster,* in my opinion justifies at least a subgeneric distinction for these two species. The relatively small size of the papulae themselves, the marked size difference of some of the plates (including the primary ones) on the disc and arm bases and the development of spines several millimetres long on some of these plates provide supporting characters. At least two of the non-Atlantic species currently listed as *Luidiaster* can be placed in this subgenus, for which I propose the name *Christopheraster.* These are: *Pontaster oxyacanthus* Sladen, 1889, from Japan, which is very similar in abactinal armament to *C. blakei* and likewise has the small papular pores almost entirely offset from the midradii, and *Cheiraster horridus* Fisher, 1906, from the Hawaiian Islands, also with very small lateral papulae, a marked size difference of some of the abactinal plates and more or less enlarged spines on the larger plates (Fig. 2g & h). The holotype of *oxyacanthus* at R 73 mm has two large subambulacral spines on most plates, while that of *horridus* at R 35 mm has two subequal spines, so that the tendency to develop a second subambulacral spine, more or less accelerated in different species, may also be used to distinguish the subgenus.

Secondly, the unusual combination in *C. echinulatus* of rather low, polygonal, closely-fitting abactinal plates armed over most of their surface with relatively numerous short spinules, dorsally broad superomarginals, unlike *Cheiraster* (*Luidiaster*), usually slender marginal spines, unlike the conical ones of *Cheiraster* (*Cheiraster*), and multiple subambulacral spines in all but the smallest specimens (R <20 mm), also justifies a subgeneric distinction I believe. The name *Barbadosaster* (again reflecting the type locality of the type species) seems appropriate. In this case the subgenus appears to be monotypic. One non-Atlantic species of *Cheiraster—Pontaster teres* Sladen, 1889, from the Banda Sea, East Indies, superficially resembles *C.* (*Barbadosaster*) *echinulatus* in the slender marginal spines and multiple subambulacrals but differs markedly in the pore areas.

CHEIRASTER Studer

Archaster (pt.) Perrier, 1875 : 348 [1876 : 268] (*A. echinulatus*); 1884 : 256; Verrill, 1885*a* : 151.

Cheiraster Studer, 1883 : 129; 1884 : 49–50; Perrier, 1885 (pt.) : 70; 1894 : 275; Fisher, 1906 : 1040; Ludwig, 1910 : 440, 454–457; Fisher, 1911 : 120, 123; Verrill, 1915 : 123–124; Fisher, 1919 : 190–191; H. L. Clark, 1941 : 26; Downey, 1973 : 40–41; Jangoux, 1978 : 95, Walenkamp, 1979 : 23.

Luidiaster Studer, 1883 : 131 [nom. nud., no species named]; 1884 : 46–47; Ludwig, 1910 : 440–441, 451–454; Fisher, 1911 : 127; Verrill, 1915 : 149–150; Fisher, 1940 : 96; H. L. Clark, 1941 : 28. [Type species: *Luidiaster hirsutus* Studer, 1884.]

Pontaster (pt.) Sladen, 1885 : 610; 1889 : 23–27; Verrill, 1894 : 247; 1895 : 131.

Acantharchaster Verrill, 1894 : 268–269. [Type species: *Archaster dawsoni* Verrill, 1880.]

Pectinaster: Verrill, 1915 : 137–139; Downey, 1973 : 43; Walenkamp, 1979 : 26. [Non *Pectinaster* Perrier, 1885.]

TYPE SPECIES. *Cheiraster gazellae* Studer, 1883, by subsequent designation by Ludwig, 1910.

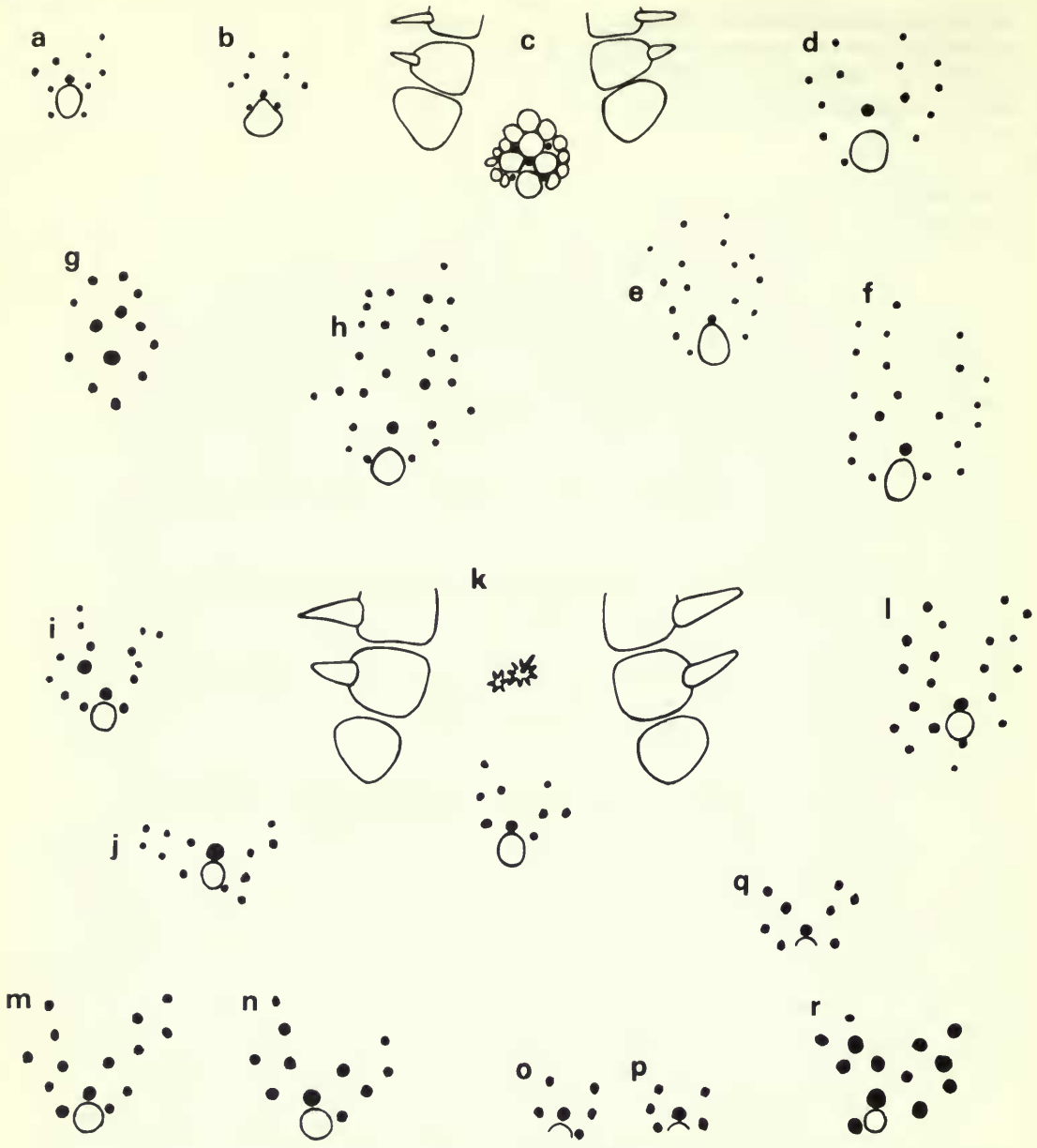


Fig. 4 Pore arrangements, showing presumed primary radial plates. (a–h) *Cheiraster (Barbadosaster) echinulatus* (Perrier). (a) *Blake* st. 45, MCZ 2181, R 27 mm; (b) *Albatross* st. 2322, USNM 10109, R *c.* 30 mm; (c) *Blake* st. 36, MCZ 24, R *c.* 20 mm (with proximal superomarginals); (d–f) *Atlantis* st. 2981C or 2982C, MCZ 3917, R 48, 47 and 51 mm; (g) holotype of *C. vincenti* Perrier, *Blake* st. 231, R *c.* 42 mm; (h) *Atlantis* st. 3480 or 3482, MCZ 3924, R *c.* 55 mm. (i–r) *Cheiraster (Cheiraster) sepitus* (Verrill), (i) 'topotype', *Albatross* st. 2075, USNM 24525, R *c.* 37 mm; (j) holotype of *Pectinaster dispar* Verrill, *Albatross* st. 2751, USNM 18468, R *c.* 50 mm; (k) *Albatross* st. 2531, USNM 12062, R 35–40 mm (with proximal superomarginals); (l) holotype of *Pontaster perplexus* Perrier, *Talisman* 1883, st. 96, PM 3378, R 52 mm; (m, n) holotype of *Luidiaster dubius* H. L. Clark, *Atlantis* st. 3326, MCZ 3815, R *c.* 60 mm; (o, p) *Princesse Alice* st. 743 (Azores), MCZ 2689, R 22 mm; (q) same sample (named *Pontaster venustus* by Koehler, 1909), R *c.* 33 mm; (r) *Talisman* 1883, st. 93, MCZ 30, R *c.* 45 mm (named *P. venustus* by Perrier, 1894).

(In fact, the spelling of the specific name in 1883 was *Gazella*, emended in 1884 to the genitive.)

A genus of Benthopectinidae without odd interradial marginal plates; abactinal plates usually parapaxilliform, more or less convex but flatter on the arms and sometimes all low, armed with several spinules, in most species many midradial and disc plates with a larger central spinelet, sometimes a spine >2 mm long; papular pores limited to a bilobed area at the base of each arm, or sometimes a pair of lateral areas loosely integrated at their proximal ends medially, rarely the two lobes not well defined or asymmetrical, undeveloped in younger animals, R <*c.* 30 mm, only the plates in the median proximal part of the area somewhat deepened; superomarginal plates aligned partially on the dorsal surface and forming a more or less broad frame to the paxillar area (except in *Cheiraster* (*Luidiaster*) where they are inconspicuous), armed usually with a single conical or spike-like spine on the dorso-lateral convexity; inferomarginal plates sometimes with more than one large spine or graduated spinelets below the main spine; adambulacral plates with the convex or angular furrow margins armed with a fan of slender furrow spines, the arc usually continuous with a few similar but smaller proximal and distal spines, partly surrounding one, two, or several, more or less enlarged subambulacral spines, similar in shape and size to the marginal spines; fasciculate pedicellariae usually present, at least on some actinal plates, often also abactinally and on the lower faces of the inferomarginals adjoining the adambulacrals, rare in a few species (e.g. *C. sepitus*), mostly bipectinate (i.e. arising from two adjacent plates) but the inferomarginal ones often lack an adambulacral component. Dorsal muscle bands of arms are attached proximally to one or two ambulacral plates, which may have modified ridges, the adjacent marginals and sometimes also to the dorsal body wall distal to the papular area.

Subgenus ***CHEIRASTER*** Studer, 1883

A subgenus with abactinal plates parapaxilliform convex and rounded, even those on the disc only abutting loosely together, most proximal and mid-radial ones armed with a central spinelet among the smaller spinules; papulae including a median proximal primary one, distinct from the rest (except in some larger specimens, R >50 mm) by its larger size and position, which is at first distal to the primary radial plate though may become dissociated from it as other plates develop, the later developed pores at first forming a median patch and then extending into a distal lobe on each side; superomarginal plates forming a more or less broad frame to the paxillar area in dorsal view; marginal spines conspicuous, conical or spike-like, some species with a second but smaller inferomarginal spine; adambulacral plates predominantly with single subambulacral spines, similar in shape to the marginal ones, though the first plate and some distal plates may develop a second large spine.

Type species. *Cheiraster gazellae* Studer, 1883. Philippines—NW Australia: 360–470 metres.

Other species included. In chronological order:

Archaster sepitus Verrill, 1885	North and Central Atlantic	485–3700 metres
Pontaster pilosus Alcock, 1893	South of India	1080–1310 metres
C. inops Fisher, 1906	Hawaiian Is to Sri Lanka	430–1250 metres
C. snyderi Fisher, 1906	Hawaiian Is–Nicobar Is	420–1670 metres
C. niasicus Ludwig, 1910	Philippines–Celebes	485–930 metres
C. ludwigi Fisher, 1913	Indonesia	1270 metres
C. triplacanthus Fisher, 1913	Celebes & South-east Africa	1050–1280 metres
C. planus Verrill, 1915	Gulf of Mexico–French Guiana	550–715 metres
C. diomedeae Fisher, 1917	Philippines	770 metres
C. weberi Döderlein, 1921	Indonesia	470 metres
C. otagoensis McKnight, 1973	South New Zealand	1000–1280 metres

(A specimen from off Natal with R *c.* 40 mm referred to *C. triplacanthus* (A. M. Clark, 1977),

has distinctly enlarged primary papular pores; Fisher (1919) noted only that the pore areas in the holotype (R 49 mm) are 'double and joined only at the adcentral end'.)

Subgenus *LUIDIASTER* Studer, 1884

A subgenus of *Cheiraster* with abactinal plates parapaxilliform, even those on the disc rounded and abutting loosely together or more or less spaced, most of the larger plates, even laterally on the arms, armed with a central spinelet among the smaller spinules; papulae including a median proximal primary one but this probably soon became indistinguishable as the number of pores increases and the areas spread, though are still bilobed; superomarginal plates aligned mainly laterally, inconspicuous dorsally; marginal spines conspicuous, conical or spike-like, usually at least two on most inferomarginal plates; adambulacral plates with two or more large subambulacral spines, the furrow angle variable.

TYPE SPECIES. *Luidiaster hirsutus* Studer, 1884. Kerguelen, South Africa & Bouvet I.; 240–550 metres.

OTHER SPECIES INCLUDED. In chronological order:

Archaster dawsoni Verrill, 1880	Bering Sea–British Columbia	100–290 metres
Pontaster planeta Sladen, 1889	S. Chile, Argentina–Falklands	350–450 metres
Cheiraster gerlachei Ludwig, 1903	Antarctic	160–810 metres
Pectinaster robustus A. H. Clark, 1917†	Chile	2410 metres
Luidiaster tuberculatus Djakonov, 1929	Japan Sea	140–850 metres

† See p. 121.

Subgenus *BARBADOSASTER* nov.*

A subgenus of *Cheiraster* with most proximal abactinal plates polygonal in outline, fitting closely together and not markedly convex, sometimes almost flat, armed with relatively numerous short spinules, on the larger plates often forming two rings around a central spinelet; papulae including a median proximal primary one, usually distinct from the rest by its size and position, the later developed pores forming at first a median patch, then extending distally into a lobe on each side, though the two lobes may be unequal or ill-defined, hardly separated medially; superomarginal plates forming a broad frame to the paxillar area in dorsal view; marginal spines slender, not very stout basally, single, though some enlarged spinelets develop below the inferomarginal spine; most adambulacral plates with more than one subambulacral spine, except in very small specimens, R <20 mm, the furrow angle of the proximal plates markedly acute.

TYPE SPECIES. *Archaster echinulatus* Perrier, 1875. South Florida—Caribbean; 150–570 metres. Monotypic.

Subgenus *CHRISTOPHERASTER* nov.*

A subgenus of *Cheiraster* with the abactinal plates parapaxilliform (but in *C. mirabilis* only slightly convex), distal plates more or less spaced, the proximal plates mostly fitting fairly closely, very variable in size, the primary central, radial and interradial plates particularly enlarged, some or most of the larger plates armed with a central spine >2 mm long, often conspicuous, surrounded by small spinules, some other plates may have a central spinelet

*Named after the type localities of the relevant type species: Barbados for *C. (B.) echinulatus* and St. Christopher's (Kitts) for *C. (C.) mirabilis*.

but not in *C. mirabilis*; no primary midradial papular pore, the first-formed papulae a pair, each latero-distal to the primary radial plate, later pores developing laterally and distally, the two pore areas on each ray only loosely meeting proximally in larger specimens to form a single diffuse bilobed area with few, if any, midradial pores, the pores themselves relatively small and hardly visible with the naked eye, relatively numerous (*c.* 100 at R 100 mm on each ray); superomarginal plates partly aligned dorsally, forming a narrow frame to the abactinal area but becoming inconspicuous in the largest specimens (R > 120 mm); marginal spines large and spike-like; adambulacral plates with one or two large subambulacral spines, sometimes two only in the largest specimens, furrow angles variable in prominence.

TYPE SPECIES. *Archaster mirabilis* Perrier, 1881. Florida—Windward Is; 380–730 metres.

OTHER SPECIES INCLUDED. In chronological order:

Cheiraster blakei sp. nov.	Florida–Northern Brazil	250–1030 metres
Pontaster oxyacanthus Sladen, 1889	Southern Japan	630 metres
C. horridus Fisher, 1906	Hawaiian Is	260–330 metres

This leaves a residue of the following species of uncertain affinities which have been referred to *Cheiraster* or *Luidiaster*:

Cheiraster pedicellaris Studer, 1883. NE of Australia; 1000 metres. The holotype has R *c.* 30 mm and is probably a young specimen of *C. gazellae* according to Ludwig (1910).

Pontaster subtuberculatus Sladen, 1889. SE of Australia; 1740 metres. The holotype has R only *c.* 24 mm. Like *Christopheraster* it has no mid-radial papulae, the 17–21 pores forming two irregular longitudinal rows on each side, but the pores are relatively large and there is no sign of any enlarged spinelet or spine on any abactinal plates. The arms are unusually short for a *Cheiraster* and the single marginal spines are remarkably short and blunt.

Pontaster teres Sladen, 1889. Indonesia; 260 metres. The holotype has R 42 mm and superficially resembles *C. (Barbadosaster) echinulatus,* the superomarginals being relatively broad and the marginal spines unusually slender. However, denuding part of the paxillar area shows an unusual combination of larger convex plates with flattened interstitial ones between, fitting closely together except where the relatively large papular pores are developed, at the *sides* of the arm bases. The subambulacral spines are multiple.

Pontaster trullipes Sladen, 1889. Philippines; 1920 metres. The holotype has R only 27 mm. The primary radial and interradial plates are enlarged, as in *Christopheraster,* but no large spines occur and the papulae form a median group, in which no primary one is distinct.

Pontaster cribellum Alcock, 1893. Laccadive Sea; 2200 metres. The holotype has R 45 mm. It is said to resemble *P. subtuberculatus* in lacking spinopaxillae and having relatively broad superomarginals but the papularia are small and compact, with only 5 or 6 papulae in each and the marginal spines are sharp.

Marcelaster antarcticus Koehler, 1907 (referred to *Luidiaster* by Fisher, 1940). South Orkney Is.; 3250 metres. R in the type series is up to only 33 mm. The proximal plates appear rather variable in size in the poor drawing and there are some relatively large disc spines but the papulae were not described at all so the position must remain uncertain.

Cheiraster granulatus Ludwig, 1910. 'Indian Ocean'; depth not given. Ludwig's *Valdivia* report was never completed and the only information on this barely established species is in the key distinguishing it from *C. subtuberculatus* by the numbers of inferomarginal and furrow spines and the occurrence of actinal pedicellariae, which could all be correlated with a size difference, if it was appreciably larger than the small type of *C. subtuberculatus.*

Cheiraster yodomiensis Goto, 1914 (referred to *Luidiaster* by Hayashi, 1973). Japan; 160 metres. The holotype has R 170 mm and closely resembles a *Nearchaster* in the many disc spines, laterally aligned superomarginals and great extent of the papular pores along the sides of the paxillar areas. Also the interradial superomarginal spines are relatively large and possibly asymmetrical in some interradii, judging from the photograph.

Cheiraster richardsoni Fell, 1958. Cook Strait, New Zealand; 730 metres. The holotype has R 31 mm. The superomarginals are broad dorsally and the subambulacral spines single. The papulae were undescribed.

Cheiraster monopedicellaris McKnight, 1973. Northern New Zealand; 720–770 metres. The holotype has R 39 mm. The superomarginal plates are very broad but some abactinal plates have enlarged spinelets, unlike *C. subtuberculatus*. The 3–5 papulae are said to be in a more or less V-shaped arrangement.

The complex synonymies of the North and Tropical Atlantic species are as follows:

Cheiraster (Barbadosaster) echinulatus (Perrier)
Figs 3a–f, 4a–h

Archaster echinulatus Perrier, 1875 : 348 [1876 : 269]; 1884 : 263–264, pl. 10, fig. 4.
Archaster mirabilis (pt) Perrier, 1884 : 258–259 (sts 143 & 231).
?*Cheiraster mirabilis:* Perrier, 1894 : 276–278, pl. 20, fig. 4.
Cheiraster vincenti Perrier, 1894 : 275–276.
Cheiraster echinulatus: Perrier, 1894 : 278; Verrill, 1915 : 129–130 (non pp. 131–133, pl. 14, fig. 3, pl. 19, fig. 2, pl. 25, fig. 1 ? = *C. blakei*); Downey, 1973 : 42, pl. 13, figs C, D.
Pontaster oligoporus Perrier, 1894 : 293.
Luidiaster vincenti: Ludwig, 1910 : 452, 453.
Pectinaster echinulatus: Ludwig, 1910 : 449.
Pectinaster mixtus Verrill, 1915 : 140–145, pl. 6, fig. 2, pl. 15, fig. 2, pl. 17, fig. 1; Macan, 1938 : 349 (listed); Downey, 1973 : 43–44, pl. 14, figs C, D.
Pectinaster vincenti: Verrill, 1915 : 139–140; Macan, 1938 : 349 (listed).
Pectinaster oligoporus: Verrill, 1915 : 147–148; Macan, 1938 : 349 (listed).
Luidiaster mixtus: H. L. Clark, 1941 : 29–30; A. H. Clark, 1954 : 375 (listed).

TYPE LOCALITY. Barbados, 183 metres.

RANGE. Gulf of Mexico, Florida Strait, south to Nicaragua and Venezuela, east to the Leeward Islands; 150–570 (?586) metres. (The *Atlantis* specimen from 1000 fathoms E of Cuba said by H. L. Clark (1941) to show some anomalous features, is referable to *C. sepitus*, having convex spaced abactinal plates with relatively few spinules, stout conical marginal spines, single conical subambulacral spines and relatively few, *c.* 6, furrow spines in obtusely angled series.)

Cheiraster (Christopheraster) mirabilis (Perrier)
Fig. 2a, b

Archaster mirabilis Perrier, 1881 : 27 (paragraphs 1–4 only); 1884 : 256–258, pl. 9, fig. 4 (non pp. 258–259, sts 231 & 143, pl. 10, fig. 3 = *C. echinulatus*) ?pl. 10, fig. 2 (or = *C. blakei*).
Archaster coronatus Perrier, 1884 : 262–263 (non st. 19 = *C. blakei*).
Cheiraster coronatus: Perrier, 1894 : 271–275; Ludwig, 1910 : 455, 456.
Cheiraster mirabilis (pt) Verrill, 1915 : 124–127 (non pl. 14, fig. 5 = *C. blakei*; non *C. mirabilis*: Downey, 1973, Walenkamp, 1979 = *C. planus*).
Cheiraster enoplus Verrill, 1915 : 135–137, pl. 18, fig. 1 (non *C. enoplus*: Downey, 1973 nec *Luidiaster enoplus*: H. L. Clark, 1941 = *C. blakei*)

TYPE LOCALITY. St. Kitts, Leeward Islands, 380 metres.

RANGE. SE Florida to the Windward Islands (records from the Gulf of Mexico probably mistakes for other species); 380 (?265)—1470 (usually 400–700) metres; deeper records, e.g.

Blake st. 196, 1030 *fathoms*, may be for *C. sepitus*. Uncertain identity precludes inclusion of lesser *Blake* station depths.

Cheiraster (Christopheraster) blakei sp. nov.
Figs 1b, 2c–f

Archaster coronatus (pt) Perrier, 1884 : 262 [st. 19 only].
?*Archaster mirabilis* (pt) Perrier, 1884, pl. 10, fig. 2 (non *A. mirabilis* Perrier, 1881).
Cheiraster mirabilis (pt) Verrill, 1915, pl. 14, figs 5, 5a.
Cheiraster echinulatus (pt) Verrill, 1915 : 131–133, pl. 14, fig. 3, pl. 19, fig. 2 [?pl. 25, fig. 1].
Cheiraster coronatus: H. L. Clark, 1941 : 26–27; A. H. Clark, 1954 : 375 (listed) (non *C. coronatus*: Perrier, 1894, Ludwig, 1910 = *C. mirabilis*).
Luidiaster enoplus: H. L. Clark, 1941 : 28–29 (non *C. enoplus* Verrill, 1915 = *C. mirabilis*).
Cheiraster enoplus: Downey, 1973 : 42–43, pl. 14, figs A, B.

DESCRIPTION OF HOLOTYPE. R of the only entire original arm is 118 mm (two arms with regenerating tips are 95 mm or less); r is 12 mm; R/r = 9·8/1. Arm breadth at the fifth superomarginals is 9·2 mm and the paxillar breadth here 6·0 mm, or 65%. The arms taper hardly at all for the first third of their length.

There are about 35 spines more than 2 mm long on the disc based on enlarged abactinal plates including the primary radial and interradial plates and others. An additional 10–12 smaller spines/spinelets arise in the papular area on the base of each ray, mostly on the row of plates between the two main irregular lines of pores each side of the midradial line. The longest central spines are 3·6 mm long. Only a few other abactinal plates have an enlarged central spinelet among the small slender tapering spinules, length : basal breadth *c.* 2·5 : 1. These number usually 6–14, according to the plate size, mean *c.* 10, but the enlarged disc plates have up to 20 spinules around the central spine. All the abactinal plates are markedly convex and may be called parapaxilliform; they are rounded or slightly polygonal and only butt loosely together over most of the disc, while those on the arms are spaced from each other. The papulae number *c.* 75 on each ray; only one or two proximal ones (if any) are midradial, the rest being arranged in two distally diverging bands extending from alongside the primary radial plate to level with the distal ends of the third superomarginal plates.

There are 55 superomarginals on the intact original arm, framing the paxillar area narrowly, each armed with a single spine of moderate size, the longest on the fifth and sixth plates up to 4·0 mm long, basal breadth *c.* 0·7 mm. The corresponding inferomarginal spines are similar or slightly longer, with an accessory spine about two-thirds as long below it, often also a third still smaller spine on the proximal plates besides several slender spinelets on the ventral face of the plate among the fine spinules which are of various sizes; the whole armament gives a hirsute or shaggy appearance to the plate as viewed from below.

The actinal areas are small and triangular with four or five plates along the midinterradial line on each side of which the irregular adradial series numbers only about seven plates, those bearing the pedicellariae enlarged. The actinal armament is very sparse and mixed in size with only about two spinelets/spinules on most plates.

Only 13½–15 adambulacral plates correspond to the first 10 inferomarginals. On each adambulacral no more than eight spines project over the furrow, their bases usually forming an angle of *c.* 90° but this may be blunted. The subambulacral spines are single, much larger and accompanied by only a few small spinules on the ventral face of the plate. The oral plates have 10 or 11 furrow spines, the apical one much enlarged and the second one intermediate. Probably only one suboral spine is enlarged but the plates are badly rubbed and most spines lost.

Pectinate pedicellariae are developed on the adradial actinal plates (usually four in each interradius), on the ventral sides of the inferomarginals adjacent to the adambulacrals (for about three-quarters of the arm length) and abactinally (but only two are present near the centre of the disc).

VARIATIONS. Some indications of variations and growth changes can be derived from Table

Table 4 *Cheiraster (Christopheraster) mirabilis* (Perrier). Measurements (in mm) and counts from various specimens including the holotypes of *C. enoplus* Verrill (the first specimen) and *mirabilis*, data from Verrill and Perrier respectively.

Station	R	r	R/r	No. of pores/ray	No. of disc spines	No. of s.m. plates	Length of 4th s.m. spine	No. of furrow spines	No. of subamb. spines
Alb. st. 2128 (Verrill)	185	21	8·8	400+ [?]	*c.* 15	*c.* 60	15	10–12	1 to 2
Gerda st. 917	110	13	8·5	88	9	49	–	10,11	1
Gerda st. 694	105	12·5	8·4	*c.* 80	10	58	13	12	1
Gerda st. 1012	*c.* 95	12	*c.* 8	98	6	40+	–	9	1
Blake Holotype (Perrier)	87	12	7·25	*c.* 73	6–10	40+	–	10	1
Pillsbury st. 944	85	10	8·5	*c.* 95	7	47	–	10	1
Pillsbury st. 918	82	10·5	7·8	58	4	46	–	9	1–1 (2)
Atlantis st. 3444	72	–	–	39	5	–	12	–	–
Pillsbury st. 889	70	8·5	8·2	*c.* 48	12	39	–	9	1 (2)
USNM no. 3741, Puerto Rico	*c.* 68	9	*c.* 7·5	50–60	7	–	–	–	1
Gerda st. 235	68	9	7·5	39,41	18	38	9·7	9,10	1 (2)
Pillsbury st. 891	50	·7	7·1	31	7	36	–	9	1 (2)
Gerda st 694	*c.* 45	6	*c.* 7·5	27,28	2	–	6·3	8–10	1
Gerda st. 694	39	5	7·8	17	5	30	2·8	7,8	1
Gerda st. 1008	31	5	6·2	18	6	26	*c.* 3·5	7,8	1

Table 5 *Cheiraster (Christopheraster) blakei* sp. nov. Measurements (in mm) and counts from various specimens.

Station	R	r	R/r	No. of pores/ray	No. of disc spines	No. of s.m. plates	Length of longest s.m. spine	No. of furrow spines	No. of subamb. spines
Pillsbury st. 607	*c.* 130	15	*c.* 6·7	*c.* 160	few	–	*c.* 6	–	1
Gerda st. 918 Holotype	118	12	9·8	*c.* 75	35+	55	4·0	7,8	1
Atlantis st. 2963F	112	13	8·6	*c.* 80	*c.* 75	–	5·5	8,9	(1) to 2
Pillsbury st. 607	*c.* 110	13	8·5	*c.* 80	*c.* 16	–	*c.* 5	*c.* 9	1
Gerda st. 403	77	11	7·0	*c.* 66	*c.* 16	39	3·8	*c.* 9	1
Oregon st. 4226	*c.* 70	12	*c.* 5·8	56	–	–	*c.* 4	*c.* 10	2 (1)
Gerda st. 403	65	10	6·5	73	17	38	3·3	7	1
Gerda st. 403	63	9	7·0	29	*c.* 14	36	2·6	9	1
Oregon st. 4226	45	8	5·6	–	*c.* 7	–	–	*c.* 9	1 (2)
Gerda st. 403	45	8	5·6	*c.* 27	*c.* 14	30	–	7 (8)	1
Gerda st. 403	44	7·5	5·9	34	17	28	3·4	8	1
Silver Bay st. 1184	38	8·5	4·5	33	22	27	3·2	9	1
Pillsbury st. 587	33	7·0	4·7	14	*c.* 18	26	–	8	1

5. The disc is usually relatively larger than in the holotype and the arms more often taper evenly from the base, with the superomarginals forming a somewhat wider frame to the paxillar area, though never making up as much as 50% of the arm breadth. Often many abactinal paxillae have an enlarged central spinelet, graduating in size to the small spines on the papular areas. The relative number of papulae also varies; one specimen has well over 100/ray even though R does not exceed 100 mm. In small specimens, the first one or two pores appear at R *c.* 16 mm (at the same time as the genital pores which are adjacent to the first superomarginal plates). 20 specimens with R 14–19 mm show a range in pore/ray number of 0–11 but with a mean of only 3. The marginal spines may be relatively larger than in the holotype, up to *c.* 6 mm long at R >100 mm. In small specimens the fourth superomarginal spine is the largest but the fifth and sixth ones grow allometrically to equal and then exceed it. The number of adambulacral plates corresponding to the first ten inferomarginals is usually more than in the holotype, often 16 or up to 18 being noted. The bases of the furrow spines usually form a more pronounced angle projecting over the furrow. Finally, the occurrence of pedicellariae varies; some specimens may have more numerous abactinal ones; also at least one was observed with inter-superomarginal pedicellariae interradially.

AFFINITIES. *Cheiraster (Christopheraster) blakei* is closely related to *C. (C.) mirabilis.* Most of the differences are expressed in the tabular key (Table 3), the numerical tables here (Tables 4 and 5) and the comparison on pp. 104–5. These can be summed up as differences in armament, *C. mirabilis* having the enlarged abactinal and marginal spines relatively larger but fewer than *C. blakei* and the abactinal and inferomarginal spinules short and more nearly uniform. Additionally, the furrow spines tend to be more numerous in *C. mirabilis,* their arrangement on the furrow margin less angular and the contours of the abactinal plates lower.

TYPE LOCALITY. *Gerda* st. 918, 26° 03′ N, 78° 05′ W, between Florida and the Bahamas, 804–822 metres. To be deposited in the U.S. National Museum.

RANGE. Recorded from SE of Florida and the coasts of Cuba east and south to the Lesser Antilles and northern Brazil at least as far east as 44° W; 250 (?225)–1033 (but mostly 500–800) metres.

Cheiraster (Cheiraster) planus Verrill
Fig. 5a, b

Cheiraster planus Verrill, 1915 : 133–135, pl. 18, fig. 2.

Pectinaster gracilis Verrill, 1915 : 145–147, pl. 6, fig. 1, pl. 14, fig. 4, pl. 15, fig. 1; Macan, 1938 : 349 (listed); Jangoux, 1978 : 95–96, fig. 2A, B. (?*P. gracilis*: Walenkamp, 1979 : 26–30, figs 9, 10, pl. 5, figs 1–4, pl. 6, figs 1–4).

Cheiraster mirabilis: Downey, 1973 : 41–42, pl. 13, figs A, B; Walenkamp, 1979 : 23–26, figs 8, 10, pl. 4, figs 2–4 (non *C. mirabilis* (Perrier, 1881)).

TYPE LOCALITY. Unknown to Verrill but the holotype (USNM 18469) may have been from *Albatross* st. 2396 (Gulf of Mexico between the Mississippi delta and Cedar Keys) from which there is a sample (USNM 10564) including another specimen of *C. planus* (named *mirabilis* by Verrill but probably at an earlier date) and a note saying '17 specimens lent to A. E. Verrill'.

RANGE. Western Gulf of Mexico and SW Caribbean, eastwards south of Jamaica to the Lesser Antilles and along the north coast of South America to French Guyana; 550 (?408)–715 (?824) metres. A record from SW of Florida, *Gerda* st. 439, *c.* 24° N, 82½° W, needs confirmation since even the larger of the two specimens has R only 16 mm; the superomarginal spines appear to be larger than the inferomarginal ones, the abactinal plates are convex, the inferomarginals have fairly uniform spinules and the furrow angles of the adambulacrals are relatively shallow, as in *C. planus* as opposed to *C. echinulatus.* However, most of the distinctive subambulacral spines are lost.

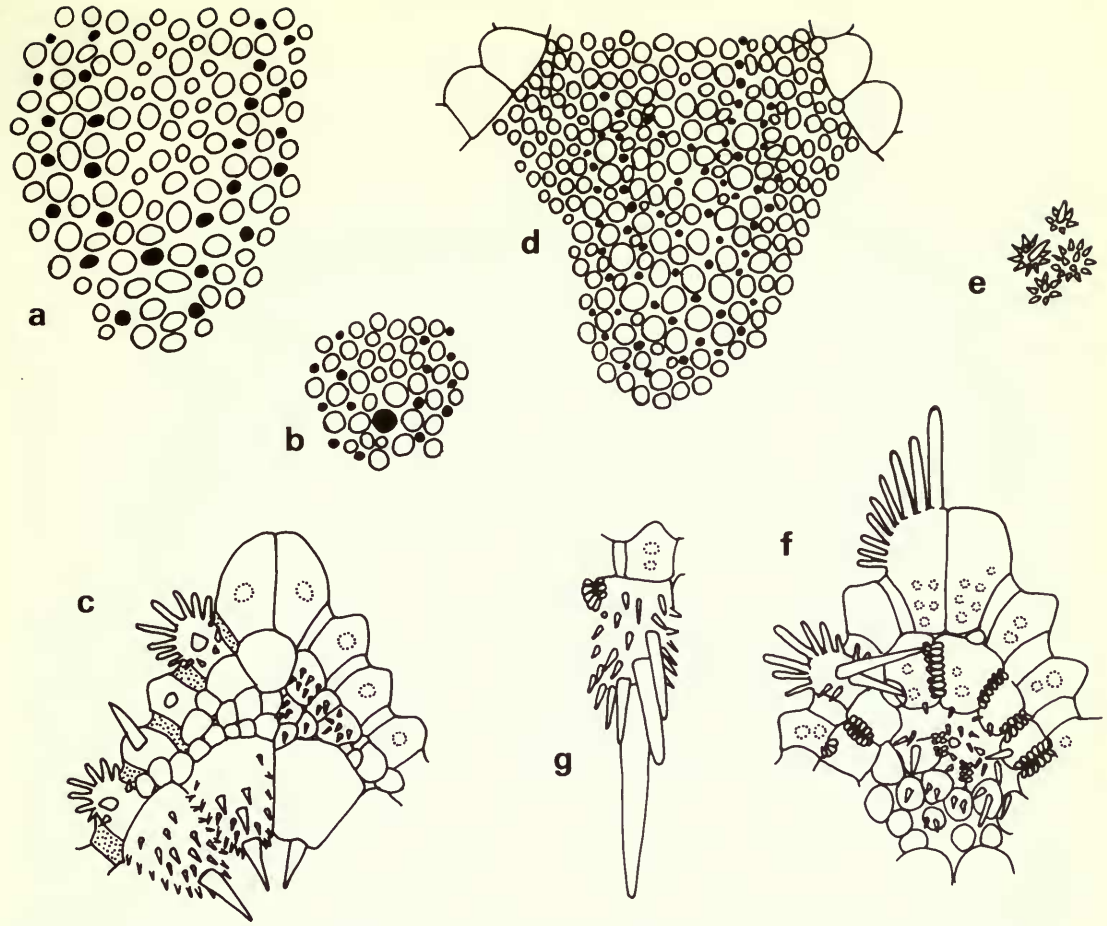


Fig. 5 (a, b) Pore areas of *Cheiraster (Cheiraster) planus* Verrill; (a) holotype, *Albatross* (st. ?), USNM 18469, R 92 mm; (b) *Albatross* st. 2396, USNM 10564, R *c.* 60 mm (same sample as holotype of *Pectinaster gracilis* Verrill); (c) *Cheiraster (Cheiraster) sepitus* (Verrill), ventral interradius partly denuded, same specimen as in fig. 4(k), the sockets of the missing subambulacral and suboral spines dotted; (d–g) *Cheiraster (Luidiaster) robustus* (A. H. Clark), holotype, *Albatross* st. 2789 (Chile), USNM 36945; (d) papular area and adjacent second and third superomarginals; (e) armament of four proximal abactinal plates; (f) ventral interradius, armament partly reconstructed, mostly lost; (g) fourth inferomarginal and adjacent adambulacral plates.

Cheiraster (Cheiraster) sepitus (Verrill)
Figs 4i–r, 5C

Archaster sepitus Verrill, 1885*a* : 151.
Pontaster venustus Sladen, 1889 : 52–55, pl. 8, figs 5, 6, pl. 12, figs 5, 6; Perrier, 1894 : 287–288; 1896 : 47; Koehler, 1909 : 14–15, pl. 1, fig. 13; Mortensen, 1927 : 71.
Pontaster venustus var. *robusta* Sladen, 1889 : 55.
Pontaster sepitus: Verrill, 1894 : 247; 1895 : 137; 1915 : 130 (footnote).
Pontaster perplexus Perrier, 1894 : 288–290, pl. 21, fig. 1, pl. 22, fig. 1; Mortensen, 1927 : 72.
Pectinaster echinulatus (pt) Ludwig, 1910 : 449 (*sepitus* a synonym).
Pectinaster dispar Verrill, 1915 : 148, pl. 14, fig. 1; Macan, 1938 : 349 (listed).
Pectinaster venustus: Koehler, 1924 : 186.
Luidiaster dubius H. L. Clark, 1941 : 30, pl. 2, fig. 2.
Luidiaster mixtus (pt) H. L. Clark, 1941 : 29–30 (specimen from 1000 fathoms).

TYPE LOCALITY. S of Cape Sable, Nova Scotia; 1570 metres.

RANGE. South of Nova Scotia south to Cuba and the Lesser Antilles, east to the Azores, Bay of Biscay [? no details, Koehler, 1924], Portugal and south to the Cape Verde area; 485–3703 metres (mostly 1000–2000 metres).

PECTINASTER Perrier

Pectinaster Perrier, 1885 : 70; 1894 : 278–279; Ludwig, 1910 : 448–451 (pt); Fisher, 1911 : 122–123; 1919 : 182; Macan, 1938 : 348–349 (pt). (non *Pectinaster*: Verrill, 1915, Downey, 1973).
Pontaster (pt) Sladen, 1889 : 43–52.

TYPE SPECIES. *Pectinaster filholi* Perrier, 1885, by subsequent designation by Ludwig, 1910. No type species was designated by Perrier in 1885 when he included two species, *Archaster insignis* Perrier, 1884 and *P. filholi* which was evidently new (though not so stated), the genus being diagnosed only by the presence of fasciculate pedicellariae (though these are relatively simple in *insignis* having up to only four spinose 'valves'). In 1894 Perrier referred *P. insignis* to *Dytaster* Sladen, 1885, leaving *P. filholi* by elimination as the only eligible type species for *Pectinaster,* the formal designation awaiting Ludwig (1910 : 449).

DIAGNOSIS. A genus of Benthopectinidae with no odd interradial marginal plates (though the paired first marginals may be a little asymmetric in some interradii of some individuals), the interradial marginal spines relatively small; abactinal plates small paxilliform, at least the proximal ones elevated medially into a more or less well defined column bearing several spinules, on most plates of the disc and midradially on the arms surrounding a larger central spinelet, the spinules tending to form a continuous surface proximally in well-preserved (and probably in live) specimens; papulae restricted to an elongate oval papularium on to each arm base, formed of specialized markedly deepened abactinal plates, convex at the upper end and abutting together laterally with flanges to accommodate the papulae (see Fig. 1a), the surface of the papularium tending to bulge upwards (at least in preserved specimens when the dorsal body wall is contracted on to the ambulacra), the first-formed pores often forming transversely-aligned pairs, three or more pores developed by a size of R 20 mm; superomarginal plates mainly aligned laterally, only forming an inconspicuous rim to the paxillar area in dorsal view, each armed with an acute conical spine at the upper end; adambulacral plates with a single large conical subambulacral spine, only the first plate sometimes with a second spine; fasciculate pedicellariae usually present, often numerous, occurring on some abactinal, marginal, actinal and even a few adambulacral plates, usually oval in outline and formed of three or more modified spinelets based on either one or (pectinate pedicellariae) on two, rarely three, plates, the valves surrounding a deep hollow or bevelled notch in the plate or plates. Dorsal muscle bands of arms attached proximally to the wings of one or two ambulacral plates laterally and the adjacent marginal plates.

REMARKS. This diagnosis emphasizing the highly modified compact oval papularia, paxilliform abactinal plates and laterally-aligned superomarginal plates not forming a wide border to the paxillar area in dorsal view, restores *Pectinaster* to the restricted concept of Perrier in 1894. As discussed under *Cheiraster*, the inclusion in *Pectinaster* of *Archaster echinulatus* Perrier, 1875, *Pontaster cribellum* Alcock, 1893, *A. sepitus* Verrill, 1885 and *Pontaster venustus* Sladen, 1889 (the last two as synonyms) by Ludwig (1910), followed by Verrill's addition in 1915 of *Pectinaster gracilis, dispar* and *mixtus* (all new nominal species) and *Pontaster oligoporus* and *Cheiraster vincenti*, both of Perrier, 1894, broadened the genus to include species with less specialized papular areas and dorsally broad superomarginal plates. All these I consider have closer affinity with the type species of *Cheiraster, C. gazellae* Studer, 1883. The type material of most of them is relatively small so that the papulae have not yet formed bilobed areas, though the enlarged median proximal pore indicates that they are potentially bilobed.

The elimination of these leaves *Pectinaster* in the Atlantic represented only by *P. filholi* and *P. pristinus* (Sladen), though the status of *P. forcipatus* (Sladen) as distinct from *P. filholi* has been debated.

In 1910, Ludwig referred *Pontaster forcipatus* Sladen, 1889, from off the eastern U.S.A., to the synonymy of *Pectinaster filholi*, type locality off Cap Blanc (with a paratype from the Azores area). He was followed in this by H. L. Clark (1923) but in 1962 I challenged this synonymy on the grounds of apparent differences in the numbers of actinal plates and their armament in the type series of *P. forcipatus* and *P. forcipatus* var. *echinata* (the latter from the Crozet Is area of the Southern Ocean), compared with Perrier's description and figures of *P. filholi* supported by a specimen (R only 33 mm) in the British Museum collections from SW of Ireland. However, after seeing further NE Atlantic specimens collected by the *Discovery*, in 1976 (Clark & Courtman-Stock) I came to agree with Ludwig and synonymize both *forcipatus* and *echinatus* with *P. filholi*, which name I used for specimens from South Africa, following H. L. Clark. Not only is there considerable variation in the numbers and shapes of the actinal plates in specimens from various parts of the Atlantic but also the records of Sibuet (1975) from the Gulf of Guinea and off Angola provide a zoogeographical link between *filholi* from NW Africa and *echinatus* from the Cape and Southern Ocean. Perrier's illustration of *P. filholi* (1894, pl. 20, fig. 3b) shows oral plates of exaggerated size at the expense of the actinal area, which appears exceptionally small, only *c.* 35% of the oral plate length, measured interradially. In four *Discovery* specimens from the Cap Blanc area (st. 9133/5) an actinal area of each measures 61, 68, 74 and 95% of the oral plate length. This compares with three specimens from W of Ireland with values of 48–92% (the minimum predictably in the smallest specimen with R only 40 mm), ten from the Gulf of Guinea off Ghana with 60–90%, six from off the U.S.A. with 65–109% and six from off South Africa and the Crozet Is area with 76–115%. The specimens with the relatively largest actinal areas, interradially longer than the oral plates, are mostly large, R > 70 mm (see Table 6).

Sladen distinguished the variety *echinata* from the type material of *P. forcipatus* by the stouter marginal spines and larger central paxillar spinelets, the occurrence of which he thought was more widespread on the lateral paxillae. In the two largest syntypes of *echinata* (R *c.* 80 mm) the fourth superomarginal spine is 1·25 and 1·15 mm in basal breadth, the latter measurement being equalled in a South African specimen with R 72 mm. In North Atlantic specimens these spines are up to 0·9–1·0 mm—a small difference but just appreciable with the naked eye. Similarly, the longest central paxillar spinelets on the disc measure 1·0 mm or more in the southern specimens as opposed to usually 0·8–0·9 mm in the northern ones, though one syntype of *P. forcipatus* has spinelets up to 1·1 mm. The extent of the central spinelets on the lateral paxillae varies also in *P. mimicus* from the Indo-West Pacific and *P. agassizi* from the East Pacific and I do not think it is a character of specific weight. Nevertheless there may be sufficient justification in the relative spinelet size for treating the southern specimens as subspecifically distinct from *P. filholi* but this should await comparison with material from the southern part of West Africa.

One regional variation which may be significant is the relative number of pores in the papularia. In the available material this reaches a maximum of 20 in the american specimens and 21 in the NE Atlantic ones. The figured syntype(s) of *P. filholi* (Perrier, 1894, pl. 20, figs 3a, 3d) shows 7 pores (only 6 in the description). A syntype in the MCZ, Harvard, with R only *c.* 45 mm, also from the Cap Blanc area, has 10 pores in one area examined. However, a *Discovery* specimen from this vicinity has as many as 21 pores in one area and 18 in another at R 65–70 mm. An even higher number is shown by some specimens of a large sample taken off Ghana by the *Pillsbury* (*c.* 4° N, 2½° W), of which 22 specimens with r > 8 mm (R probably 40+ mm) have 11–27 pores, mean 19. This compares with 6–20 pores and a mean of only 10 in 16 american specimens. Unfortunately the *Pillsbury* material is dried and in poor condition so other characters such as spinelet length cannot be ascertained in many specimens. Even in spirit-preserved specimens of *Pectinaster,* owing to frequent breakage of the arm tips, few accurate estimates of R/r or counts of marginals can be made. The mean R/r value for 16 of the type series of *P. forcipatus* is 5·9/1, compared with 5·5/1 in six

Table 6 *Pectinaster filholi* Perrier. Measurements and counts from specimens from various parts of the range. The furrow spine number and length of the central paxillar spinelets are both maxima; the actinal plate number is along the interradius. The number of adambulacral plates corresponding to the first ten inferomarginals ranges from 15–19, usually 16–18, in all the areas.

Specimen	R	r	R/r	No. of pores	4th s.m. spine br.	Act. 1./ oral 1.%	Furrow spines	Act. pls /IR no.	L. pax. spinelets
Cap Blanc area:									
Holotype (Perrier)	64	10	6·4	5,6 (7)	–	–	7	2	–
Discovery 9133/5	40 + (?*c.* 70)	13	–	*c.* 12	0·92	74	8	4	0·75
Discovery 9133/5	62 + (*c.* 65)	12	*c.* 5·4	18,21	0·85	95	7	5	0·85
Discovery 9133/5	28 + (?*c.* 50)	9	–	8	–	61	7	–	–
Talisman st. 96	*c.* 45	9·5	*c.* 4·7	10	–	–	–	–	–
W & NW of Ireland:									
Discovery 7711/85	80	14	5·7	*c.* 9	1·00	92	7	3	0·83
Discovery 7711/85	62	11	5·6	11,14	–	–	–	–	–
Discovery 7709/73	41	8	5·1	*c.* 6	–	48	5 (6)	–	–
Discovery 7709/52	40	8	5·0	6,7	–	77	6	–	–
NE U.S.A.:									
Atlantis II st. 100	37 + (?*c.* 65)	11·5	–	10	0·95	93	6	2	0·92
Syntypes of	68 + (?*c.* 80)	14·5	*c.* 5·5	10,11	0·92	96	6	3	0·83
Pontaster	60 + (?*c.* 75)	14	–	15	1·00	104	5	4	–
forcipatus	37 + (?*c.* 65)	13·5	–	13	0·71	83	5 (6)	3,4	0·92
	57 + (?*c.* 65)	12	*c.* 5·4	10	1·00	109	6	4,5	1·1
	50	11	4·5	9	–	65	7	2	–
Gulf of Guinea:									
Pillsbury st. 34	–	13	–	21	0·75	80	7	2	0·9
Pillsbury st. 34	–	12·5	–	23	–	60	8	2 (3)	–
Pillsbury st. 34	–	13	–	17	–	82	7	3	–
South Africa:									
[No data] Gilchrist	50 + (?*c.* 62)	10·5	*c.* 5·9	13	1·08	82	6 (7)	4	0·83
[No data] Gilchrist	72	14	5·1	*c.* 15	1·17	89	8	2,3	1·05
Crozet Is area:									
Syntypes of *Pontaster*	60 + (?*c.* 80)	14·5	–	17,18	1·25	100	6 (7)	5	1·00
forcipatus var.	73 + (?*c.* 82)	14	*c.* 5·9	15	1·17	115	6	4	1·17
echinata	40 + (?*c.* 55)	11·5	–	10	0·92	95	6	3	–
	52	9·5	5·5	9	0·83	76	6	2	–

specimens from the NE Atlantic but this may not be significant since the latter are mostly smaller.

As for *Pontaster pristinus* Sladen, based on a single small specimen from *Challenger* st. 325, off the River Plate, this is clearly a *Pectinaster* sensu stricto, having relatively narrow superomarginals in dorsal view and compact, slightly bulging, papularia. Reexamination of the holotype throws considerable doubt on Sladen's arguments about its distinction from *P. forcipatus*. The specimen was coated with fine mud. When this was removed, the abactinal plates of the disc were found to have clusters of up to 7 spinules, usually 4 or 5, around the fine spinelets, the tips of which were seen by Sladen, the armament being in fact indistinguishable from that of specimens of *P. filholi* of similar size (e.g. from *Challenger* st. 46, R *c.* 18 mm). (Sladen somehow misjudged R in *pristinus* as only 11·5 mm but the complete arm remaining, though curled over, is at least 5 mm longer than this. Only two pores could be found in the papularium cleared and the abactinal spinelets of the disc are up to 0·6 mm long. The condition of the arm plates is poor but does not appear to be significantly different from small specimens of *P. filholi* and the madreporite is no more conspicuous than can be attributed to adpression of the armament in its vicinity. There are 4 or 5 furrow spines on the proximal adambulacral plates with a few similar spines in series with them proximal and distal to the large conical subambulacral spine. Three North American specimens with R 18–21 mm, have 3, 4 or 6 pores in one papularium but this is probably not significant in view of the variation in pore number shown by other specimens of *filholi*. Nor do I consider the absence of pedicellariae in the single specimen of *P. pristinus* justifies a specific distinction, though pedicellariae are more or less numerous in most specimens from the NW and NE Atlantic examined.

Outside the Atlantic, *Pectinaster* includes *P. agassizi* (Ludwig, 1905) from the East Pacific and *P. mimicus* (Sladen, 1889) from the Indian Ocean, East Indies and New Zealand. Despite its having enlarged spinelets on the lateral as well as midradial abactinal arm plates and only 12–14, rather than 15–18, proximal adambulacral plates matching the first ten inferomarginals, *P. hylacanthus* Fisher, 1913, from the Philippines and Indonesia, was reduced to a subspecies of *P. mimicus* by Döderlein, 1921. If these characters are of less than specific weight, then *P. hispidus* (Woodmason & Alcock, 1891) from the Indian Ocean is also conspecific with *P. mimicus*. This synonymy is supported by comparison of a paratype of *P. hispidus* with the holotype of *P. mimicus*. Further, Macan (1938) identified several specimens from the Gulf of Aden as *P. agassizi* or *P. agassizi granuliferus* subsp. nov. rather than *P. mimicus*. The new subspecies was said to differ in having abactinal central spine(let)s on the arms restricted to the midradial areas and more granuliform spinelets on the actinal plates (besides differences in the distribution of the pedicellariae—not significant in my view), these two characters being also used by Macan to differentiate *P. mimicus* from the specimens he called *P. agassizi*. The fact that his largest specimens from the Gulf of Aden have R 119 and 158 mm could well account for the very high number of 40–50 pores in the papularia in apparent agreement with *P. agassizi* compared with up to only 20 in the few specimens attributed to *P. mimicus* in which pores have been counted (the types of *P. mimicus* with R 78 mm and of *P. mimicus palawanensis*, R *c.* 95 mm), both Fisher and Döderlein having apparently given little weight to relative pore number as taxonomically significant in *Pectinaster*. East Pacific material of *P. agassizi* has even more numerous pores—already *c.* 55 at R only 65 mm from *c.* 25 at R 45 mm, so that the number is likely to be even greater when (if) R exceeds 100 mm.

Of the other nominal species included in Macan's table for *Pectinaster*, *Pontaster cribellum* Alcock, 1893, was compared by Alcock rather with *P. subtuberculatus* Sladen, since referred to *Cheiraster*. Alcock's holotype had R only 45 mm and this could account for the still rounded rather than bilobed form of the papular areas. Finally, *Pectinaster robustus* A. H. Clark, 1917, from off Chile, has two large subambulacral spines and reexamination of the large holotype showed the pore areas (Fig. 5d) to be deeply bilobed distally and not restricted to specialized papularia. *P. robustus* is therefore now referred to the subgenus *Luidiaster* of *Cheiraster*. This action brings *robustus* into conflict as a junior secondary

Table 7 Data for the *Pillsbury* specimens of *Benthopecten*. For the abactinal spinules per proximal plate '1+' signifies an enlarged spinelet or spine on some plates; for disc spines (which tally includes enlarged spinelets more than twice as long as the ordinary spinules), C, R and I in capitals or lower case signify large or small central, primary radial and primary interradial spines, the rest being irregular in position; for pore extent, the number is the superomarginal plate opposite the distalmost pores; the adambulacral count is of the proximal ones opposite the first 10 inferomarginals; brackets around entries signify occasional occurrence.

Pillsbury station	Abactinal spinules proximal	distal	Disc spines	Pore extent	Adambs: 10 i.m. pls	Furrow spines
681, Guyana	1 + 3–10	1–6	1C,4R + *c.* 50	4	19	6–8
Basin	1–4	1–3	1C	3	19½	5
782, Colombia	3–10	–	1c,2r + 3	3	–	*c.* 6
1178, E Cuba	2–5	1–3	0	–	–	6
120, Florida/	3–6	1–3	1c,2r,2i + 2	4	16 (15)	6–8
Bermuda	1,2 (3)	1–4	1C,1r	2	21	*c.* 7
	1–4	1	2R + 3	1	19	*c.* 5
314, Gulf of	1 + 3–10	1	1C,2r + 8	5	21	7
Guinea	1–5	1–3	1C,2r,1i	4	21½	7–6
34, Gulf of	1 (2,3)	1	0	2–3	21½	6 (5,7)
Guinea	1 (2,3)	1 (2)	1c + 1	2	–	7 (8)
681, Guyana	1 (2)	1	1C,1R,2r, 3(? + 2)I + 3	3	16½	5,6 (7)

homonym with the species-group name *robusta* Sladen, 1889, originally described as a variety of *Pontaster venustus* but now referred to the synonymy of *Cheiraster (Cheiraster) sepitus* (Verrill, 1885). However, *robustus* (A. H. Clark) may well prove to be conspecific with *C. (L.) planeta* (Sladen, 1889), type locality off southern Chile, when specimens of intermediate size are available for comparison.

Turning to benthopectinids with odd interradial marginal plates, *Benthopecten* itself is well represented in the Atlantic and also in need of review.

BENTHOPECTEN Verrill

Benthopecten Verrill, 1884 : 218 (footnote); 1895 : 130; Ludwig, 1910 : 464–466; Fisher, 1911 : 142–144; Macan, 1938 : 351–352; Downey, 1973 : 40.

Pararchaster Sladen, 1885 : 610–611; 1889 : 4–7; Ludwig, 1910 : 462–464. (Type species, by monotypy, *P. pedicifer* Sladen, 1885).

TYPE SPECIES. *Benthopecten spinosus* Verrill, 1884, by monotypy.

DIAGNOSIS. A genus of Benthopectinidae with an odd interradial marginal plate in each series, usually in all five interradii, the superomarginal one more or less inset on to the disc and bearing a conspicuous spike-like vertical spine (or occasionally a cluster of *c.* 3 small spines); abactinal plates thin, flat and scale-like, at least on the arms, but sometimes convex medially on the disc, never markedly paxilliform, each bearing one or more spinules, some of which may be elongated into spinelets or even spines more than 1·5 mm long, especially

Pillsbury station	Subamb. spines	Oral f. spines	Suboral spines	Pedicellariae Abact.	Act.	i.m.	R	r
681, Guyana Basin	2	5	4	(+)	+	+	100 + (?*c.* 150)	20
	2	5,4	4	(+)	+	+	40 + (?60–70)	9·5
782, Colombia	2	6	4	+	+	+	20 ++ (?70–100)	11·5
1178, E Cuba	(1)	6	2,3	—	+	+	?? v. poor	9·5
120, Florida/ Bermuda	2 (1)	7,8	5,6	+	(+)	(+)	100	11
	1 (2)	*c.* 6	4,5 (6)	(+,1)	(+,1)	+	50 + (?*c.* 70)	9
	1 (2)	5 (4)	3 (2)	—	—	—	30	6
314, Gulf of Guinea	2	6,7	3	+	+	+	75 ++ (?*c.* 130)	19
	2	6	5	+	+	+	100 + (?*c.* 150)	20
34, Gulf of Guinea	1 (2)	6	3	+	+	+	45 + (?70–80)	9·5
	1 (2)	7 (8)	4	+	+	+	30 + (?*c.* 70)	9·0
681, Guyana	2	4,5	4	—	(+,1)	—	45 ++ (?*c.* 110)	15

on the primary plates of the disc; papulae scattered on the arm bases, usually extending further distally close to the marginal plates, so the areas become bilobed, sometimes covering much of the disc and a limited distance (usually $<\frac{1}{2}$R) along the arms; marginal plates with at least one long spine, the inferomarginals usually with an accessory spine (or two) below the main one but smaller; adambulacral plates with the furrow margin rounded or angular, armed with 3–8, sometimes more, radiating, slender furrow spines backed by one or two (rarely three) larger subambulacral spines usually aligned almost at right angles to the furrow when more than one occurs but in some species nearly parallel to it; some pectinate pedicellariae usually present, especially on the actinal plates, but often also between some abactinal or inferomarginal plates, especially proximally.

Remarks. Verrill's extraordinary omission in 1884 (though rectified in 1885*b* : 519) to mention the most obvious characteristic of *Benthopecten*—the odd interradial superomarginal plates with their conspicuous single spines—led Sladen (1885 & 1889) to refer his several species to a new nominal genus *Pararchaster*. In 1894 Verrill referred *Pararchaster* to the synonymy of *Benthopecten*. Although Ludwig (1910) tried to retain two genera on the basis of the multiple abactinal spinelets of *Pararchaster pedicifer* Sladen, the type-species of *Pararchaster*, as opposed to the single ones of *Benthopecten spinosus*, Fisher (1911) found this distinction untenable at the generic level, following observations on the more abundant North Pacific material available to him. Study of the material of *Benthopecten* collected in the deep tropical Atlantic by the *Pillsbury* raises new doubts about even the specific significance of the frequency of the abactinal armament in many cases. These new specimens

yield the data included in Table 7, from which it is evident that the very small samples collected at stations as wide apart as the Gulf of Guinea off West Africa, the Guyana Basin off northern South America (outside the Antillean chain) and the North American Basin between Florida and Bermuda, show a wide range within each sample in abactinal spinule frequency. The maximum spinule number is found in one large specimen from st. 681 off Guyana and another from st. 314 in the Gulf of Guinea, each sample including a second specimen with much less dense armament but otherwise not significantly different. St. 120 also includes one more spinulose specimen out of three, though the difference is less marked. However, a third specimen was collected at st. 681; this is the single individual, segregated in Table 7, having the minimum of abactinal spinelets—rarely more than one, which may be specifically distinct. Such a conclusion is supported by its primary *interradial* disc spines appearing to be better developed than the primary radial ones, coupled with there being rarely as many as 7 furrow spines (and that only on odd plates), where 6 or 7 is the usual number in the other specimens, and only a single (actinal) pedicellaria, where all the rest with R > 50 mm have several actinal and inferomarginal pedicellariae and usually also some abactinal ones. A review of the fairly abundant material of *Benthopecten spinosus* from the eastern continental slope of the U.S.A. has shown a consistent agreement in these same characters, except that the rare pedicellariae found were only on the inferomarginal and not the actinal plates.

In comparison with other Atlantic species, a multispinulose condition with up to 10 spinules on some abactinal disc plates is shown by the four syntypes of *B. spinosissimus* (Sladen) from off Ascension I (R 60–68 mm) and the holotype of *B. fischeri* (Perrier) from NW Africa (R *c.* 40 mm), the latter reexamined at the Paris Museum.

In *B. spinosissimus* already at R < 70 mm the papulae extend distally to level with the sixth or seventh superomarginals and the marginals themselves are relatively short and numerous, numbering 47–53 in each series in the syntypes, giving a ratio of 1·2–1·4/1 for R/SM number. This compares with only about 30 marginals and a ratio of *c.* 2·2/1 at this size in *B. spinosus* and probably a similar number in *B. simplex* (Perrier), of which a specimen with an intact arm showing R 55 mm has only 25 superomarginals, also giving a ratio of 2·2/1. A further distinction of *B. spinosissimus* is the small number of furrow spines, only 3 or 4 on each plate, leaving little doubt of its specific distinction.

With regard to *B. fischeri*, I found the holotype and only recorded specimen to have 4 or 5 spinules on most proximal abactinal plates but additional ones on some plates with an enlarged spinelet or spine, apparently an unusually high frequency at this relatively small size. Although the jaws have a relatively rich armament of *c.* 10 furrow spines and up to 12 suboral spines and spinelets on each oral plate, there are only 6 furrow spines on most adambulacral plates and the other characters agree with the bulk of the *Pillsbury* material. (The exception is the single *Pillsbury* specimen allied with *B. spinosus,* which is quite distinct in its very sparse armament.) *B. fischeri* was referred to the synonymy of *B. spinosus* by Grieg (1921 & 1932) on its superficial resemblance.

Grieg also followed Verrill (1895) in synonymizing *Pararchaster armatus* Sladen, 1889 with *B. spinosus*, though Farran (1913) and Mortensen (1927) maintained *armatus* as a distinct species. Ludwig (1910) had instead referred *armatus* to the synonymy of *Archaster simplex* Perrier, 1881, the oldest name for any species of *Benthopecten.* The holotype (from the Gulf of Mexico NW of Cuba) has R only 18 mm and, until the *Oregon* and *Alaminos* took some rather larger specimens (R 48+ mm) in the Gulf of Mexico (described by Downey in 1973), little comparative information was available about *B. simplex.* Reexamination of these specimens and comparison with the type material of *B. armatus* from S and E of Cape Cod and various specimens from the vicinity of Portugal, SW Ireland and the Rockall Trough in the NE Atlantic reveals no differences which I consider to be significant (see Table 10). The abactinal armament is multiple in all except immature specimens (numbering usually 1–5 spinules on the proximal plates), the disc spines (when developed) tend to enlarge first on the primary radial more than the interradial plates, the number of furrow spines averages 6 or 7 on most of the adambulacral plate series and the number of sub-

ambulacral spines tends to increase from one to two with size, with occasional exceptions; lastly there is a relatively high incidence of pedicellariae, often in all three loci, in all but the smaller specimens (R <40 mm), again with some individual variation.

The origin of some of the *Pillsbury* specimens from areas geographically adjacent to the Gulf of Mexico (the nearest being from st. 1178 east of Cuba) and their morphological resemblance to the rather smaller and mostly less well preserved *Oregon* and *Alaminos* specimens reinforces belief that all can be referred to *B. simplex* but for the exceptional specimen from st. 681 which is indistinguishable from *B. spinosus*. This serves both to extend the known size range of *B. simplex* to R *c.* 150 mm and also to extend the geographical range (not unexpectedly in view of the great depths) not only to both sides of the North Atlantic but also both sides of the tropical Atlantic, including the Gulf of Guinea, taking in the type locality of *Benthopecten chardyi* Sibuet, 1975. Despite several peculiarities of Sibuet's unique holotype (discussed further below), it seems to fall within the range of variation of *B. simplex*.

Characters. Apart from the density of the abactinal armament (now considered to be of only limited use) the following characters have been adopted as of some taxonomic significance in distinguishing the species of *Benthopecten*:

1. The development of enlarged spines on the centre of the disc (by Ludwig)
2. The relative size of any accessory spines on the inferomarginal plates (Sladen, Ludwig and Fisher)
3. The number of paired marginal plates in each series (Sladen)
4. The numbers of furrow and subambulacral spines (Sladen *et al.*)
5. The number of oral furrow spines (Ludwig)
6. The number of adambulacral plates corresponding to the first ten paired inferomarginal plates (Ludwig and Macan, 1938)
7. The occurrence of pedicellariae (Sladen *et al.*)
8. The presence of more than one superomarginal spine (Sladen and Macan)
9. The substitution of several small spines for the usual conspicuous odd interradial superomarginal spine (Perrier, 1894, for *B. folini*)
10. The extent of papulae along the arm (Fisher and Macan)
11. The extent of the inferomarginal pedicellariae along the arm (Fisher and Macan)
12. The number of actinal pedicellariae (Macan)

Other characters which can be considered as possibly significant for some of the species but needing further comparisons for appreciation of their wider significance within the whole genus are:

13. The occasional non-bifurcation of the papular areas distally
14. The relative size of the primary radial and interradial disc spines, when developed
15. The number of suboral spines
16. The presence of more than one series of actinal plates and
17. The relative size of the first paired superomarginal spines.

Fortunately, since the arms are rarely preserved intact, the R/r ratio does not appear to be taxonomically significant in this genus, the relative disc size being apparently variable over a similar range in all the species. As in many long-armed asteroids, the R/r ratio tends to increase allometrically with absolute size.

As with the characters based on the abundance of abactinal spinules, most of the others are subject to some degree of variation.

No. 1, the development of enlarged spines on the disc, depends to some extent on size and is also subject to variation. For instance, in large specimens of *B. spinosus*, R >90 mm, the disc spines range from few and inconspicuous, <1·5 mm long, to a cluster of 20 or more, some exceeding 6 mm in length. An elaboration of this is character no. 14, the relative size of the primary radial and interradial disc spines, when developed, studied now only in *B. spinosus* and *B. simplex*, where a range of specimens is available. As detailed under the heading of *B. simplex*, on average the primary radial spines in that species are equal to or

slightly larger than the primary interradial ones, whereas in *B. spinosus* the interradial spines are mostly better developed (not counting those of the madreporic interradius where the spine development is generally erratic). This character remains to be evaluated in other species.

No. 2, the mean size of the accessory inferomarginal spine (if developed) relative to the main spine above it, appears to be somewhat variable and is of uncertain value because of paucity of information about its range, only holotypes having often been described. In some species such as *B. spinosus* it seems to be fairly consistently at least half as long as the main spine, whereas in *B. simplex* the reverse is true and it rarely exceeds half the spine length. (An exception again is the holotype of *B. chardyi* where the accessory spine is often large and may even equal the main spine on some plates.) Very spinose species such as *B. spinosissimus* have several successive accessory spines on each plate, graduating in size.

No. 3, the number of marginals relative to R, remains to be investigated for most species, marginal counts having rarely been cited by authors, partly because so few specimens are usually obtained with any arms intact. The development of additional marginal plates adjacent to the terminal does not keep pace with the elongation of the arms so that the ratio of R/SM number tends to increase with R. In 12 specimens of *B. spinosus* with R 35–155 mm, the ratio ranges from 1·8/1 (in the smallest) to 3·4/1 (in the largest), whereas nine specimens with R 70–110 mm have a range of 2·3–3·0/1 and a mean of 2·6/1. The holotype of the closely related *B. semisquamatus* (Sladen), from Japan, does not differ significantly, having a ratio of 3·0/1 at R 166 mm. In contrast, as mentioned above, the four syntypes of *B. spinosissimus* with R 60–68 mm have a ratio of only 1·2–1·4/1, the marginals being relatively short and more numerous, 47–53, as opposed to only 32 in a specimen of *B. spinosus* with R 73 mm.

No. 4, the numbers of furrow and subambulacral spines, may show a wide range along the furrow length of a single specimen, usually tending to increase beyond the proximal plates and to a greater extent in very large specimens. For instance, in the holotype of *B. heteracanthus* Macan from the Indian Ocean, R 210 mm, the number increases from 7 or 8 proximally to 11 on many distal plates, while the holotype of *B. polyctenius* Fisher from Indonesia, at R 224 mm, has a range from 9–14. Two smaller specimens of *B. polyctenius* with R 120 and 80 mm have lower maxima of 11 and 9 respectively. In species of more restricted size range, the range in furrow spine number is probably restricted to *c.* 3 or 4. For instance, in *B. spinosus*, known to reach R 155 mm, the range is 4–6, predominantly 5, even in larger specimens, R >90 mm, while *B. simplex* with a similar size range usually has 6 or 7, occasionally 5 or 8 spines. The holotype of *B. chardyi* Sibuet (now thought to be less than specifically distinct from *B. simplex*) has 5 or even 4 spines on about the first ten adambulacral plates but the number increases first to 6 then 7 beyond about the twentieth plate. As for the subambulacral spine number, up to a size of R 30 mm *B. simplex* has only single spines on nearly all the plates, then in most specimens a second spine becomes enlarged beyond the most proximal plates so that specimens with R >60 mm usually have two subambulacrals predominating throughout the series. (The holotype of *B. chardyi* with single spines on most plates could be interpreted as neotenous in this respect; two slightly smaller specimens of *B. simplex* also from the Gulf of Guinea have a small second spine on some plates.)

No. 5, the number of oral furrow spines, would be expected to vary through the same sort of range as the mean number of adambulacral furrow spines. Certainly *B. polyctenius* shows a range of 8–14 according to Fisher (1919). *B. spinosus* has 5 or 6, occasionally 4, and *B. simplex* shows a range from 5 to 8, compared with 10 (or even 11) oral furrow spines in the holotype and only mature specimen of *B. fischeri* (Perrier) at R only *c.* 40 mm, which in other respects resembles the more spinulose specimens of *B. simplex* and has only *c.* 6 furrow spines on the adambulacral plates. Until more material from the type locality of *B. fischeri* is available, the significance of this character remains to be determined.

No. 6, the number of adambulacral plates relative to the first ten paired inferomarginals, appears to vary over a range of 4 or 5, sometimes more, in a single species (see Tables 9, 10),

judging from the data available. Unfortunately, even Ludwig, who initiated its use, failed to cite it for several species and not all subsequent authors have included counts in their descriptions. The usual number in *B. spinosus* is 17–20, while in *B. simplex* between 18 and 21 is common but as many as 24 (or even 25) are found, for instance in the anomalous holotype of *B. chardyi*. Also in the holotype of *B. violaceus* (Alcock) from the Indian Ocean 24 are supposedly found but this number is derived only from the drawing, not Alcock's description, and may not be correct.

Nos 7, 11 and 12. The occurrence and frequency of pedicellariae are notoriously variable and rarely reliable in diagnosing most asteroid species; this is equally true of *Benthopecten*. Only a large sample (rarely provided) can give a good idea of the relative frequencies of abactinal, actinal and inferomarginal pedicellariae. Even in *B. spinosus*, in which pedicellariae have long been thought to be consistently rare or absent, an additional sample of ten specimens from the *Atlantis II* collections showed four with at least some inferomarginal pedicellariae.

No. 8, the presence of accessory superomarginal spines in species such as *B. spinosissimus* is correlated with a generally higher frequency of spines on all the plates and is not in itself significant.

No. 9, the absence of conspicuous spines from the odd interradial superomarginal plates, as described in *B. folini* (Perrier, 1894), from off NW Africa, is not shown by all specimens of the type series so one must conclude that either two sympatric species were included or that the character is variable. If there are two species in the type series, the one with multiple diminutive spines on the odd plates also usually has two subambulacral spines. The other, with single large spines may have one subambulacral spine and is then indistinguishable from *B. simplex chardyi*. It is not certain which specimen in the Paris Museum collections Perrier used for his full description; the arms were broken and he could only cite r, which he gave as 12 mm. The largest specimen from off Cap Blanc (*Talisman* 1883 haul 96, P.M. no. 3304) is almost certainly the one shown in Perrier's pl. 19, figs 1a and 1b of a general view, above and below; I estimate its r as 10·0–10·5 mm (some shrinkage during nearly 100 years in spirit is not unlikely); R is 65 + ?10–20 mm; all the odd superomarginals have small spines and there are two subequal subambulacral spines on most plates. Of the two specimens from haul 98, slightly further south (P.M. nos 3317 and 3318) one has had the abactinal body wall removed and is the specimen so mutilated shown in Perrier's pl. 20, fig. 1c. The second has R50 + ?20–30 mm, r *c.* 11 mm and so could be the specimen from which pl. 20, figs 1a and 1b of details of parts of the disc were made, though there are some divergencies between the finer details of armament and Perrier's description. Accordingly, the largest specimen from off Cap Blanc is now designated as lectotype; its subambulacral armament was probably misrepresented as single in pl. 19, fig. 1a by Perrier's artist. However, of the four (not three) smaller and more broken specimens from this same haul 96, one has relatively large single odd superomarginal spines up to 6 mm long, R being 20 + ?*c.* 30 mm; its subambulacral spines are mostly single. The other three are more damaged interradially, the spines of the odd plates mostly lost; one has a pair of large spines still attached to one plate and signs of paired spines in at least two other interradii. From *Talisman* haul 97 (no. 3305) come three more damaged paratypes, at least one with three massive single odd superomarginal spines.

Possibly these large spines are vulnerable to damage or loss from the attacks of predators and the anomalies in development are due to differential regeneration. In the holotype of *B. pikei* H. E. S. Clark, 1969, from New Zealand, in four out of five interradii the spines are relatively small and in 1970 she suggested that this might be attributable to injury when she described a variety *australis* of *B. pikei* from two specimens with all the odd spines large.

No. 10, the distal extent of the papulae along the arms, progresses during growth, usually from level with the first superomarginal to the third or fourth, while the distalmost pores are usually lateral rather than midradial (character no. 13). However, in *B. acanthonotus* Fisher, from off California, the distal extremity varies in three large specimens from level with the fifth superomarginal to the twentieth. In this species the papular areas are consistently bifurcating but the holotype and only described specimen of *B. indicus* Koehler, from off Sri

Table 8 Tabular key to the species of *Benthopecten* known from the Atlantic.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
spinosus	1 (2)	+I	S	3,4	L	½–⅔	16½–20	4,5 (6)	2	5 (6)	3,4 (5)	—	—	(+)	155
simplex chardyi	1 (2–4)	—	S	3	L	¾	24–25	(4) 5–7	1	(5) 6,7	3,4	+	+	+	90–100
simplex simplex	1–5/ + 3–10	+/(+)R	S	2–5	L	¼–⅓	16–23	6,7	1,2	5,6	3,4	(+)	+	+	*c.* 150
folini	1 (2,3)	(+)	S	4	Sm	*c.* ½	?*c.* 20	7 (8,9)	2 (1)	7	4	+	+	+	75–80
fischeri	1 + 3–10	(+)	M	4	L	*c.* ½	20–21	*c.* 6	2	10 (11)	*c.* 12	—	+	+	39
spinosissimus	1 + 2–10	(+)	M	6,7	L	⅔–¾	19–23	3 (4)	2	8	3,4 (+ 2)	—	+	(+)	70

Tables 8 and 9 Tabular keys to the Atlantic and non-Atlantic species of *Benthopecten*.

1. Armament of most proximal abactinal plates: simple numbers indicate the number of spinules; 1+ signifies an enlarged spinelet or spine in addition to some spinules; () signifies occasional numbers
2. Occurrence of central disc spines > 1·5 mm long: + well developed, > 10; (+) inconspicuous, *c.* 5; — lacking (except sometimes for a single anal spine); I primary interradial ones larger; R primary radial ones larger
3. Number of spinules on abactinal arm plates beyond papular areas: S single; M multiple
4. Superomarginal opposite distalmost papular pores
5. Size of odd superomarginal spine: S small; M moderate; L large; m multiple (otherwise single)
6. Length of accessory inferomarginal spine relative to that of the main spine
7. Number of adambulacral plates corresponding to the first 10 paired inferomarginals
8. Number of furrow spines
9. Number of subambulacral spines
10. Number of oral furrow spines
11. Number of suboral spines
12. Occurrence of abactinal pedicellariae: (+) signifies rare; ++ very numerous
13. Occurrence of actinal pedicellariae
14. Occurrence of inferomarginal pedicellariae
15. Maximum R of specimens recorded or now studied

Table 9 Tabular key to the non-Atlantic species of *Benthopecten*.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	General area
semisquamatus	1	+	S	4	L	$\frac{3}{4}$–$\frac{7}{8}$	16	4–5	2	4–5	3	–	–	–	166	Japan
*huddlestoni**	1	+	S	4	L	?	?17	6–8	$2\frac{1}{2}$	6–7	3	–	+	+	*c.* 170	Indian Ocean
moluccanus	1	+	S	3	L	*c.* $\frac{7}{8}$	19,20	7–9	2	5–8	3–5	++	+/–	+	80	East Indies
pikei	1(–4)	+	M?	4,5	M	'shorter'	?	5–8	2 (3)	5–7	7–10	–	+	(+)	*c.* 80	New Zealand
pectinifer	1	(+)	S	5	L	?	18	5,6 (7)	2	6–8	4,5	+	+	+	160+	East Pacific
heteracanthus	1(–4)	(+)	S	6	L	$\frac{1}{2}$–$\frac{2}{3}$	17–18	7–11	2	6	3	–	+	+	210	Indian Ocean
pedicifer	1–4	(+) R	M	4	M	$\frac{2}{3}$	17,19	(6) 7,8	3 (2)	7 (6)	6,7	++	+	+	168	Southern "
styracius	1–3	(+)	M	3	L	$\frac{1}{2}$–$\frac{3}{4}$	19–22	7,8	2 ($+\frac{1}{2}$)	6	3	++	+	+	105	Philippines
incertus	1 (2,3)	–	?	?	?L	0	?	4	2	4,5	?	–	–	–	'young'	Indian Ocean
*violaceus**	2–4	–	M	2	L	*c.* $\frac{1}{2}$	?24,25	7,8	2	7,8	2	–	–	(+)	*c.* 100	Indian Ocean
pikei v. *australis*	3–6	+	M	?	L	?	?	6	2	4,5	?	?–	(+)	+	150	New Zealand
cognatus†	2–4(–12)	(+)	M	5	L	0	15,16	6 (5)	2	6	?	++	(+)	+	160	East Pacific
indicus	1 or 6–10	+	M	12	L	?	?	3	2	?	?	+	+	–	*c.* 120	Indian Ocean
claviger	1 + 8–15	+	M	5,6	M–L	*c.* $\frac{7}{8}$	19	4–6	2	5,6	6	+	+	+	110	North Pacific
acanthonotus	1 + 1–6	+ (+)	S	5–20	L	$\frac{1}{2}$–$\frac{2}{3}$	?	4,5 (–7)	2	4,5	4,5	+ (+)	+ (+)	(+)	164+	East Pacific
rhopalophorus	1 + ?5–9	+	M	5,6	L	?*c.* $\frac{7}{8}$	?	5–7	2	?	?	–	(+)	–	130	N-w Pacific
munidae	1 + 2–5	'small'	M	7,8	L	?	?	5–7	2	11,12	4,5	–	+	–	45	New Zealand
spinuliger†	1 + 3–12	(+)	M	3	L	?$\frac{1}{2}$	20	5 (4)	1 (2)	13–15	3–5	(+)	+	+	75	East Pacific
polyctenius	1 + 10+	(+)	M	4	Mm	'shorter'	20	8–14	2 ($+\frac{1}{2}$)	7,8	3–5	++	+	++	225	East Indies

**B. huddlestoni* and *B. violaceus*: the entry in column 6 depends on the accuracy of the artist of the *Investigator* illustrations.
†*B. cognatus* and *B. spinuliger*: the entries in column 1 (and 3 for *cognatus*) are based on re-examination of the type material.
B. pentacanthus Fell, 1958, is omitted since the holotype had R only 5 mm and could only show juvenile characters common to most of the species.

Lanka (R *c.* 120 mm) has the papulae extending to superomarginal 12 for the whole width of the arm. In a *Pillsbury* specimen from NE of Florida (R 100 mm), now referred to *B. simplex,* the papulae extend to the fourth superomarginals and the areas do not bifurcate. Also in the holotype of *B. chardyi* the distalmost pores are adradial rather than abradial and extend only to the third superomarginal though R is 90–100 mm. However, two slightly smaller *Pillsbury* specimens also from the Gulf of Guinea have the areas bifurcating; their papulae extend distally to the third (or even the distal ends of the second) superomarginals. Isolated cases of non-bifurcating areas have been recorded from at least one non-Atlantic species and proper scrutiny of more material may well show occasional instances of this, suggesting that character 13 has little taxonomic significance. Since in some benthopectinids the dorsal arm muscles are attached at least partially to the dorsal body wall near the base of the arm, as well as or rather than to the ambulacrals and marginals, this might have a limiting effect on the extent of the pores medially.

No. 15, the number of suboral spines, is usually 3 or 4 (sometimes 5) on each plate in most species, accompanying spinelets being rare. Occasionally higher numbers are found. Reexamination of the holotype of *B. fischeri* from NW Africa showed a total of *c.* 12 suboral spines and spinelets on each plate, four of them distinctly larger than the furrow spines. In contrast, the four similarly multispinose syntypes of *B. spinosissimus* from near Ascension Island have only 4 suboral spines on most plates, though there may be one or two additional spinelets on some plates. The oral furrow spines on the type of *B. fischeri* are also unusually numerous, as discussed under character 5.

No. 16, the number of series of actinal plates, is correlated with the relative disc size, as well as tending to increase with growth. Until an R of *c.* 100 mm, rarely more than one series is well developed. More larger specimens are needed to evaluate this character.

No. 17, the relative size of the first paired superomarginal spines, shows a considerable range from very reduced in comparison with the fourth (usually the largest) spine to almost as large as the odd interradial spine. It can result in very different appearances of the interradii but preliminary observations suggest that it is too variable (even within one specimen) to be significant.

The characters thought to be most useful are utilized in two tabular keys (Tables 8 and 9) to distinguish the Atlantic and non-Atlantic species of *Benthopecten.* Analysis of these tables shows only very minor differences in variable or largely untested characters between several of the nominal species or differences possibly attributable to growth changes; notably *B. spinosus* Verrill and *B. semisquamatus* (Sladen) are separated only by an insignificant difference in the number of adambulacrals relative to the inferomarginals. The occasional presence of inferomarginal pedicellariae in *B. spinosus* may well prove to be shared by some specimens of *B. semisquamatus* other than the syntypes, when more material is available for comparison. This close affinity was observed by Sladen, who treated an east American specimen, now regarded as conspecific with *B. spinosus*, as only a variety *occidentalis* of *B. semisquamatus*. Inter-oceanic distributions of abyssal species such as these are very likely. If the present decision to treat Atlantic specimens showing a considerable range of variation in density of the abactinal armament as a single species, *B. simplex*, is proved correct, then barriers to the conspecificity of many nominal species in the middle and lower parts of Table 9 will be almost completely broken down and there should be a drastic reduction in the number of valid species of *Benthopecten* recognized.

Since *Benthopecten simplex* is the first-named species of the genus and its limits—both morphological and geographical—are considerably extended by the *Pillsbury* and other specimens now considered to be referable to it, a full account of this species is given here.

Benthopecten simplex (Perrier)

Archaster simplex Perrier, 1881 : 28; 1884 : 264, pl. 1, fig. 8.
Pararchaster armatus Sladen, 1889 : 19–22, pl. 1, figs 5, 6, pl. 4, figs 5, 6.
Pararchaster simplex: Perrier, 1894 : 253, 254–256.

'*Pararchaster* nov. sp. (*P. Fischeri* Perrier aff.)' Mortensen *in* Schmidt, 1904 : 24.
Benthopecten simplex: Ludwig, 1910 : 461, 464, 465, 466; Fisher, 1911 : 143; Verrill, 1915 : 122; Downey, 1973 : 40, pl. 12, figs C, D.
Benthopecten armatus: Farran, 1913 : 2–3; Mortensen, 1927 : 74–75, fig. 41.
Benthopecten spinosus (pt) Grieg, 1921 (& 1932) : 12–13, pl. 4, fig. 1 (*Michael Sars* sts 95 & 101 at least); H. L. Clark, 1941 : 26. (Non *B. spinosus* Verrill, 1884).
Benthopecten chardyi Sibuet, 1975 : 283, 289–291, fig. 3, pl. 1, figs B, D

R is probably up to *c.* 150 mm but rarely more than 80 mm; R/r is 7·7–7·9/1 and R/no. of superomarginal plates *c.* 2·25/1 in three specimens with R 50–55 mm.

Diagnosis. A species of *Benthopecten* with multiple spinules on most proximal abactinal plates, often 2 or 3 but sometimes up to *c.* 10 when they are accompanied by a larger spinelet or spine, especially at R > *c.* 50 mm, those on the primary radial plates tending to be better developed than those of the primary interradial plates; papular areas usually distally bifurcate, the distalmost pores level with the second or third superomarginals in specimens with R 50–80 mm but extending to the fourth or even the fifth in those with R > 100 mm; odd interradial superomarginal plates with a single very large spine, other superomarginals also with single spines and a few small spinelets or spinules, inferomarginals with an accessory spine below the main one but usually less than half as long; 16–23, usually 18–21 proximal adambulacral plates corresponding to the first ten paired inferomarginals (though up to 25 in the holotype of *B. chardyi*); actinal plates few, a second series only developed at R > 100 mm; adambulacral plates with 6 or 7 furrow spines (sometimes 5 or 8) and one or two subambulacral spines, usually two at R > 50 mm beyond the first ten or so plates, where there is more often only a single spine; oral plates with 5 or 6 (sometimes 4 or 7) furrow spines and 3 or 4 (5) suboral spines; actinal and some inferomarginal pedicellariae usually present at R > 50 mm and sometimes also some abactinal ones.

Variations. As mentioned under the generic heading, the armament of the abactinal plates is very variable in *B. simplex,* if I am right to include most of the *Pillsbury* specimens. At R 50–70 mm there are usually 2 or 3 (1–5) spinules on the proximal plates and single ones on the plates distal to the pore areas but occasional specimens of this size and larger ones may have some proximal plates enlarged with a bigger spinelet and up to 10 spinules.

The degree of enlargement of spinelets and spines is also variable. Even at R *c.* 70 mm there may be only a single central spine appreciably larger than the spinules, though usually several others may exceed 1·5 mm in length at this body size, especially on some of the primary plates.

The papular areas normally bifurcate distally but the largest specimen from *Pillsbury* st. 120, NE of Florida, has the distalmost pores adradial.

The odd interradial superomarginal spines are usually very conspicuous but on occasional specimens one or more of them may be reduced in size.

The length of the accessory inferomarginal spine is usually less than half that of the main spine but it may be lacking altogether on most plates of a few individuals or conversely be nearly equal in length to the main spine on some plates, e.g. of the paratype of *Pararchaster armatus* with R 42 mm from *Challenger* st. 46—but not in the larger paratype from the same station.

In larger specimens the single subambulacral spines of the proximal adambulacral plates often give way to two spines beyond, as in Downey's specimens from the Gulf of Mexico, shown by reexamination.

Other variants are mentioned in the diagnosis.

Synonymy. Until Downey (1973) described some *Oregon* and *Alaminos* specimens of *B. simplex* from the Gulf of Mexico, only the juvenile holotype (R 18 mm) had been described from the West Indian area and it was difficult to establish whether Sladen's type material of *Pararchaster armatus* from SE and E of Cape Cod (*c.* 42° N, 63° W and 40° N, 66° W) is synonymous with *B. simplex*, as proposed by Ludwig (1910) or with *B. spinosus* Verrill, also

Table 10 *Benthopecten simplex* (Perrier) and a comparable specimen of *B. spinosus* Verrill. Disc spine abbreviations as in Table 7. Specimen 19 is included for comparison with Perrier's description of the holotype. *Sarsia* st. 7627 is in the southern Bay of Biscay.

Specimen and station	Proximal abactinal spinelets	Disc spines	Adambs: 10 first i.m. plates	Furrow spines	Subamb. spines	Oral furrow spines	Pedicellariae Abact.	Act.	i.m.	R (mm)	r (mm)
(1) *Oregon* st. 2574	2,3 (1–5)	1C,2R,1I + 10	18	7 (8)	2	6	–	+	(+)	*c.* 80	11·5
(2) *Oregon* st. 2574	1–3	1C,3R,1i + 7	–	6	2	5,6	–	+	–	*c.* 80	11·0
(3) *Oregon* st. 2574	3,4 (5)	1C,2R,1I + 3	–	7	2	6	–	+	+	*c.* 70	10·0
(4) *Oregon* st. 2574	1–5	1C + 1	–	6	1,2	5	–	+	–	–	9·0
(5) *Challenger* st. 46	2,3 (1–5)	3R + 4	20	7,8	1	6	(+)	+	–	*c.* 70	8·5
(6) *Alaminos* st. 46	1–5	1C,4R,4I + 5	20	6 (7)	1,2	5	–	(+)	–	*c.* 70	8·0
(7) *Alaminos* st. 46	1 (2,3)	1C,2R,2I	–	7	?	–	–	+	++	–	8·0
(8) *Oregon* st. 2574	1 (2,3)	2	21	6 (5)	1	5	–	–	–	*c.* 65	7·0
(9) *Challenger* st. 46	1 (2–4)	4	18	4,5	1 (2)	6	–	+	–	45	8·0
(10) *Alaminos* st. 4	1 (2,3)	1C,1R,1r + 1	19	7	2	5	–	–	+	55	7·0
(11) *Alaminos* st. 4	2 (1–3)	1C,2R,2I + 4	19	7 (6) 9	1,2	?	(+)	+	+	45	7·0
(12) *Alaminos* st. 4	1,2 (3)	1C,3R,1I	20,21	6 (5)	1 (2)	5	–	+	+	50	6·5
(13) *Alaminos* st. 4	1 (2)	1C,1R,1I + 8	19	6 (5)	2 (1)	4	(+)	+	++	50	6·5
(14) Rockall Trough	2,3 (1–5)	1c	20	7 (6)	1	6 (5)	–	++	–	*c.* 50	8·0*
(15) *Challenger* st. 50	1 (–5)	1c	20	6	1	5	(+)	+	–	37	6·5
(16) SW Ireland	2,3 (1–5)	0	23	5	1	6	–	–	–	40	6·0
(17) *Alaminos* st. 4	1 (2,3)	1c	–	?	1,2	4 (5)	–	(+)	–	35	6·0
(18) *Sarsia* st. 7627	1,2 (3,4)	1C,1R	18½	5	1	5	(+)	–	–	33	6·5
(19) *Alaminos* st. 4	1 (2,3)	–	–	3,4	1,2	4	–	–	–	16	3·5
(20) HOLOTYPE	1?	–	–	4,5	1	–	–	–	–	18	3·4
B. spinosus *Albatross* st. 2221	1	3r,4I	20	4 (3,5)	2	5,6	–	–	–	55	8·0

*This specimen has only four rays.

from the eastern U.S.A., as proposed by Verrill (1895). Comparison of the larger specimens of Downey and Sladen, together with a few further individuals from the NE Atlantic (off Portugal, the Bay of Biscay, SW Ireland and the Rockall Trough) yields the data shown in Table 10, which also includes for comparison the only available specimen of *B. spinosus* of comparable size. Table 7 of the *Pillsbury* specimens, all but one now referred to *B. simplex,* should also be consulted.

Although the positions of the disc spines and enlarged spinelets are often irregular (especially adjoining the madreporic interradius), the contrast in the specimen of *B. spinosus* in Table 10 of four relatively large primary interradial spines with the three smaller primary radial spines (reflected also by most large specimens of *B. spinosus*) is very marked, as well as the absence of multiple abactinal spinules. Further, the presence of only 4 furrow spines on most adambulacral plates, as compared with the usual 6 or 7 of *B. simplex,* and the total absence of pedicellariae, combine to justify treating *B. simplex* as distinct from *B. spinosus* in my view and at the same time synonymizing *B. armatus* with *B. simplex*. In fact, two smaller american paratypes of *P. armatus* (R *c.* 40 and 30 mm) and the portuguese paratype (R *c.* 32 mm) do have only 5 or sometimes 4 furrow spines but this is to be expected at this size and is probably only transitory. Also occasional larger specimens of *B. simplex* lack pedicellariae and conversely a few specimens of *B. spinosus* do have some inferomarginal ones.

With regard to the relationship of *B. chardyi* Sibuet with *B. simplex*, Sibuet had only a single specimen, from the Gulf of Guinea off Gabon (*Jean Charcot* st. CY 19, *c.* 2½° S, 8° E, 2584 m.), R90–100 mm, which has been reexamined. It has only a few inconspicuous spinelets enlarged near the anus, no disc spines, the papular areas do not bifurcate distally (not observed by Sibuet), the accessory inferomarginal spines are relatively large, sometimes almost equal in length to the main spine, there are as many as 24 or 25 adambulacrals corresponding to the first ten inferomarginals (not noted by Sibuet) and the subambulacral spines are almost without exception single; the furrow spines number 6 or 7 on most plates—as usual in *B. simplex*—the 4 or 5 recorded by Sibuet being limited to some of the proximal plates and transitional to the higher numbers. Apart from the last, the combination of these characters has not otherwise been found in *B. simplex* but each of them individually is liable to vary. Two (poorly preserved) specimens also from the Gulf of Guinea but to the NW off Ghana (*Pillsbury* st. 34, *c.* 4° N, 2½° W, *c.* 1970 m) with R *c.* 70 mm have a majority of the adambulacral plates with one rather than two subambulacral spines. However, one of them has two small disc spines developed, their papular areas are bifurcating, the accessory inferomarginal spines were probably relatively small and there are only 21½ adambulacrals matching the first ten inferomarginals on the only arm of which sufficient remains to allow a count. Two much larger specimens again from the Gulf of Guinea but off western Nigeria (*Pillsbury* st. 314, *c.* 5° N, 4° E, 2300 m), R ?130–150 mm, both have only a single disc spine and a few enlarged spinelets, the pore areas bifurcate, the accessory inferomarginal spines are less than half as long as the main spine and there are only *c.* 21 adambulacrals corresponding to the first ten inferomarginals but the subambulacral spines are predominantly two. These few specimens indicate that in the Gulf of Guinea at least, the development of disc spines and a second subambulacral spine is relatively retarded. Whether or not this is sufficiently consistent to justify retention of *B. chardyi* as a distinct taxon remains to be seen from further material. At present it seems best to treat it as a subspecies of *B. simplex.*

Similar doubts about the specific validity of *B. folini* must exist considering the inclusion in the type material of at least two specimens with conspicuous large odd superomarginal spines interradially, not the small multiple spines supposed by Perrier to be characteristic of the species. (Most of the remaining paratypes have lost these spines in preservation.) The larger of these two probably had R *c.* 50 mm and the single subambulacral spines would be expected in *B. simplex* at this size. It should also be noted that the holotype of *B. chardyi* has multiple small spines on one of its five odd superomarginal plates.

Since the recognition of multispinulose specimens as conspecific with *B. simplex,* only the numerous oral furrow and suboral spines in the holotype of *B. fischeri* at R only *c.* 40 mm

serve to distinguish it. In spite of this and the presence of two subambulacral spines on most proximal plates, I think it not unlikely that further material from the type locality off NW Africa will show the holotype to be only an aberrant *B. simplex.*

RANGE. From the vicinity of Cape Cod (42–40° N, 63–66° W) south to the Gulf of Mexico, the Colombia and Guyana Basins and from south of Iceland (*Thor* st. 164) and the Rockall Trough (*c.* 57° N, 10° W) south to the Gulf of Guinea (*c.* 2½° S, 8° E); 1175–2585 metres.

Acknowledgements

Most of the observations on material of the U.S. National Museum and the Museum of Comparative Zoology, Harvard, were made during a visit in 1953/54 but I am indebted to Miss M. E. Downey and Professor R. M. Woollacott of those institutions for recent loans of specimens; also to Professor A. Guille, of the Paris Museum.

References

Alcock, A. 1893. An account of the collection of deep-sea Asteroidea. ('Investigator'). *Ann. Mag. nat. Hist.* **11** : 73–121, pls 4–6.

Clark, A. H. 1916. Six new starfishes from the Gulf of California and adjacent waters. *Proc. biol. Soc. Wash.* **29** : 51–62.

—— 1917. Three new starfish and one new brittle-star from Chile. *Proc. biol. Soc. Wash.* **30** : 151–158.

—— 1954. Echinoderms (other than holothurians) of the Gulf of Mexico. *Bull. US Fish Commn* **55** : 373–379.

Clark, A. M. 1962. Asteroidea. *Rep. B.A.N.Z. Antarctic Res. Exped.* **B9** : 1–104, 18 figs, 5 pls.

—— 1977. The South African Museum's *Meiring Naude* cruises. 4. Echinoderms. *Ann. S. Afr. Mus.* **73** (6) : 133–147.

—— **& Courtman-Stock, J.** 1976. *The echinoderms of southern Africa.* British Museum (Nat. Hist.) Publ. no. 776, 277 pp., 276 figs. London.

Clark, H. E. S. 1969. Two new species of *Benthopecten* (Asteroidea) from New Zealand. *Trans. R. Soc. N.Z.* (Biol.) **11** : 83–88, 1 fig., 1 pl.

—— 1970. Sea stars (Echinodermata : Asteroidea) from 'Eltanin' cruise 26, with a review of the New Zealand asteroid fauna. *Zool. Publs Vict. Univ.* no. 52: 1–34, 3 figs, 3 pls.

Clark, H. L. 1923. The echinoderm fauna of South Africa. *Annls S. Afr. Mus.* **13** : 221–435, 4 figs, pls 8–13.

—— 1926. Echinoderms from the South African Fisheries and Marine Biological Survey. 2. Sea-stars (Asteroidea). *Rep. Fish. mar. biol. Surv. Un. S. Afr.* no. 4. Spec. Rep. no. 7 : 1–34, 7 pls.

—— 1941. Reports on the scientific results of the Atlantis Expeditions to the West Indies. The echinoderms (other than holothurians). *Mem. Soc. cubana Hist. nat.* **15** (1) : 1–54, 10 pls.

Döderlein, L. 1921. Die Asteriden der Siboga-Expedition. 1. Porcellanasteridae, Astropectinidae, Benthopectinidae. *Siboga Exped.* **46**[1] : 1–47, 7 figs, 13 pls.

Downey, M. E. 1973. Starfishes from the Caribbean and the Gulf of Mexico. *Smithson Contr. Zool.* no. 126 : 1–158, 48 pls.

Farran, G. P. 1913. The deep-water Asteroidea, Ophiuroidea and Echinoidea of the west coast of Ireland. *Scient. Invest. Fish. Brch Ire.* **1912** (6) : 1–66, 17 figs, 2 pls.

Fisher, W. K. 1906. The starfishes of the Hawaiian Islands. *Bull. U.S. Fish. Commn* **1903** (3) : 987–1130, 49 pls.

—— 1910. New starfishes from the North Pacific. *Zool. Anz.* **35** : 545–553; 568–574.

—— 1911. Asteroidea of the North Pacific and adjacent waters. 1. Phanerozonia and Spinulosa. *Bull. U.S. natn. Mus.* **76** (1) : 1–419, 122 pls.

—— 1919. Starfishes of the Philippine Seas and adjacent waters. *Bull. U.S. natn. Mus.* **100** (3) : 1–546, 156 pls.

—— 1940. Asteroidea. *Discovery Rep.* **20** : 69–306, 23 pls.

Goto, S. 1914. A descriptive monograph of Japanese Asteroidea. *J. Coll. Sci. imp. Univ. Tokyo* **29** : 1–808, 19 pls.

Grieg, J. A. 1921 [reprinted 1932]. Echinodermata. *Rep. scient. Results Michael Sars N. Atlant. deep Sea Exped.* **3** (2) : 1–47, 5 pls.

Hayashi, R. 1973. *The sea-stars of Sagami Bay: collected by His Majesty the Emperor of Japan.* Biological Laboratory, Imperial Household of Japan. xi + 114 pp., 13 figs, 18 pls.

Jangoux, M. 1978. Les étoiles de mer (Echinodermata : Asteroidea) récoltées par le M/V *Calamar* au large des Guyanes et du Venezuela. *Bull. zool. Mus. Univ. Amsterdam* **6** (13) : 93–101, 3 figs.

Koehler, R. 1907. Astéries, Ophiures et Echinides recueillis dans les mers australes par la *Scotia. Zool. Anz.* **32** (6) : 140–147.

—— 1909. Echinodermes provenant des campagnes du yacht *Princesse-Alice. Result. Camp. scient. Prince Albert* **34** : 1–317, 32 pls.

—— 1924. *Les echinodermes de mers d'Europe.* 1.xiii + 360 pp., 9 pls. Paris.

Ludwig, H. 1903. Seesterne. *Résult. Voy. Belgica* (Zool.) 72 pp., 7 pls.

—— 1910. Notomyota, eine neue Ordnung des Seesterne. *Sber. preuss. Akad. Wiss.* **23** : 435–466.

Macan, T. T. 1938. Asteroidea. *Scient. Rep. John Murray Exped.* **4** (9) : 323–435, 12 figs, 6 pls.

McKnight, D. G. 1975. Classification of somasteroids and asteroids (Asterozoa: Echinodermata). *Jl R. Soc. N.Z.* **5** : 13–19.

Mortensen, T. 1904. *In* Schmidt, J. Fiskeriundersøgelser ved Island og Færøerne i Sommeren 1903. *Skr. Kommn Havunders.,* Kbh. no. 1 : 16–24.

—— 1927. *Handbook of the echinoderms of the British Isles.* ix + 471 pp., 269 figs. London.

Okutani, T. 1969. Synopsis of bathyal and abyssal megalo-invertebrates from Sagami Bay and the south off Boso Peninsula trawled by the R/V Soyo-Maru. *Bull. Tokai reg. Fish. Res. Lab.* no. 57 : 1–61, 22 figs, 8 pls.

Perrier, E. 1875. *Revision de la collection de Stellérides du Museum d'Histoire Naturelle de Paris.* 384 pp. Paris. [Also published in: *Archs Zool. exp. gén.* **4** (1875) : 265–450; **5** (1876) : 1–104, 209–309.]

—— 1881. Description sommaire des espèces nouvelles d'Astéries. *Bull. Mus. comp. Zool. Harv.* **9** : 1–31.

—— 1884. Mémoire sur les étoiles de mer recuillies dans la Mer des Antilles et le Golfe de Mexique. *Nouv. Archs Mus. Hist. nat. Paris* (2) **6** : 127–276, 10 pls.

—— 1885. Première note préliminaire sur les Echinodermes recueillis durant les campagnes de dragages sous-marins du *Travailleur* et du *Talisman. Annls Sci. nat.* (6) **19** (8) : 1–72.

—— 1894. Stellerides. *Expéd. scient. Travailleur-Talisman.* 431 pp., 26 pls.

—— 1896. Contribution à l'étude des Stellérides de l'Atlantique Nord. *Result. Camp. scient. Prince Albert* **11** : 1–57, 4 pls.

Sibuet, M. 1975. Astérides abyssales de l'Atlantique sud. *Bull. Mus. natn. Hist. nat. Paris* (Zool.) no. 199 : 281–296, 3 figs, 1 pl.

Sladen, W. P. 1885. The Asteroidea. *Rep. scient. Results Voy. Challenger.* Narrative. **1** (2) : 607–617, figs 202–206.

——1889. Asteroidea. *Rep. scient. Results Voy. Challenger.* Zool. **30** : 1–935, 118 pls.

Spencer, W. K. & Wright, C. W. 1966. Asterozoans. *In* R. C. Moore, *Treatise on invertebrate paleontology,* Pt U : U4–107, 89 figs.

Studer, T. 1883. Über der Asteriden welche während der Reise S.M.S. *Gazelle* gesammelt. *Sber. Ges. naturforsch. Freunde Berlin* **1883** (8) : 128–132.

—— 1884. Verzeichniss der während der Reise S.M.S. *Gazelle* um die Erd 1874–76 gesammelten Asteriden und Euryaliden. *Phys. Abh. Akad. wiss. Berl.* **1883, 1884** (3) : 1–64, 5 pls.

Verrill, A. E. 1884. Notice of the remarkable marine fauna occupying the outer banks off the south coast of New England. No. 9. *Am. J. Sci.* **28** : 213–220.

—— 1885*a*. Notice of the remarkable marine fauna occupying the outer banks off the south coast of New England. No 11. *Am. J. Sci.* **29** : 149–157.

—— 1885*b*. Results of the explorations made by the steamer *Albatross* off the northern coast of the United States in 1883. *Rep. U.S. Fish. Commn* **1883** : 503–543, pls 13–19.

—— 1894. Descriptions of new species of starfishes and ophiurans. *Proc. U.S. natn. Mus.* **17** (1000) : 245–297.

—— 1895. Distribution of the echinoderms of north-eastern America. *Am. J. Sci.* **49** : 127–141, 199–212.

—— 1899. Revision of certain genera and species of starfishes with descriptions of new forms. *Trans. Conn. Acad. Arts Sci.* **1899** : 145–234, pls 24–30.

—— 1914. Monograph of the shallow-water starfishes of the North Pacific coast from the Arctic Ocean to California. *Harriman Alaska Ser.* **14** : 1–408, 110 pls.

—— 1915. Report on the starfishes of the West Indies, Florida and Brazil. *Bull. Labs nat. Hist. St. Univ. Ia* **7** (1) : 1–232, 29 pls.

Walenkamp, J. H. C. 1979. Asteroidea (Echinodermata) from the Guyana shelf. *Zool. Verh. Leiden* no. 170 : 1–97, 31 figs, 20 pls.

Manuscript accepted for publication 12 January 1981